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Generic revision on the *Biwia–Microphysogobio* complex (Cypriniformes, Gobionidae) with descriptions of three new genera

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Abstract

The *Biwia–Microphysogobio* complex, comprising several genera and over 40 valid species, is widely distributed in the freshwater systems of East Asia. Although many species of this complex have been discovered in the past decades, controversy regarding the taxonomic status of these genera still remains. This study revised the *Biwia–Microphysogobio* complex at the generic level. Based on the morphology of the type species in each genus and various species within this complex, the genus characteristics are described. The morphology of the lip papillae pattern, jaws, and air bladder chambers are key characteristics used to distinguish the genera. With further evidence supported by the molecular phylogenetic relationships reconstructed from mitochondrial genome sequences, each genus in this complex formed a monophyletic group. The previously polyphyletic *Microphysogobio* is now separated into four genera, rendering the newly defined genus *Microphysogobio* monophyletic. The other three genera are newly described, i.e., *Crossocheilogobio*, *Mesophysogobio*, and *Oriengobio*. Along with *Biwia*, *Huigobio*, and *Platysmacheilus*, the complex now includes seven genera. The distribution of each genus is mapped separately in this study. A diagnostic key to genera is provided, and species included in each genus are listed. Sixteen new combinations are generated in this study.

Key Words

East Asia, freshwater fish, morphology, mtDNA genome, phylogeny

Introduction

Pseudogobionini is a group of freshwater fish under the family Gobionidae in the order Cypriniformes (Yang et al. 2006; Tang et al. 2011; Tan and Armbruster 2018; Chen et al. 2023). Possessing developed lips with affiliated apparatus, reduced air bladders, and horizontally expanded pectoral fins, they are true benthic dwellers of Gobionidae, inhabiting various freshwater habitats such as mountain streams, rivers, and lakes across East Asia (Yue 1998). Comprehensive reviews of Pseudogobionini have been carried out through systematic studies of Gobionidae in the past decades (Bănărescu and Nalbant 1973; Hosoya 1986; Yue 1998). Hitherto, nine valid genera and more than 80 species have been included (Zhang et al. 2020; Fricke et al. 2024), which makes Pseudogobionini the most species-rich tribe in Gobionidae. Among them, four genera, i.e., *Biwia* Jordan & Fowler, 1903, *Huigobio* Fang, 1938, *Microphysogobio* Mori, 1934, and *Platysmacheilus* Lo, Yao & Chen, 1977, exhibit the closest phylogenetic relationships (Yu and Yue 1996; Tang et al. 2011; Chen et al. 2023). Due to their shared morphological characteristics and molecular phylogenetic affinities, previous studies have debated the taxonomic status of these four genera (Jiang and Zhang 2013; Kawase 2014; Fricke et al. 2024). Some studies have treated this group of genera as a single entity (Li et al. 2018; Chen et al. 2023). Kawase (2014) named this group the "*Biwia–Microphysogobio* complex," and we have adopted this term in our study.

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The genus *Biwia* was established by Jordan and Fowler (1903) based on the type species *Pseudogobio zezera* Ishikawa, 1895, collected from Lake Biwa in Japan. Mori (1934) formally established the genus *Microphysogobio* (type species *M. hsinglungshanensis*) (Burton 1934; Sun et al. 2021). Later, Fang (1938) established the genus *Huigobio* and designated *H. chenhsienensis* Fang, 1938, as the type species. The genus *Platysmacheilus*, named by Luo et al. (1977), was established most recently based on *Saurogobio exiguus* Lin, 1932. To date, the complex encompasses over 40 valid species.

At present, one of the controversial points is the non-monophyletic nature of the genus *Microphysogobio*. Tang et al. (2011) reconstructed the molecular phylogenetic relationships of the family Gobionidae based on several nuclear and mitochondrial genes and pointed out that *Microphysogobio* was polyphyletic. In recent years, Li et al. (2018) reconstructed another phylogenetic tree based on mitochondrial genome sequences, showing that some species of *Biwia*, *Huigobio*, and *Platysmacheilus* were nested within *Microphysogobio*. Chen et al. (2023), with a phylogenetic tree including more mitochondrial genome sequences from species in Pseudogobionini, consistently suggested that the genus *Microphysogobio* is a polyphyletic group. In addition to these molecular phylogenetic studies, some taxonomic studies (e.g., Jiang and Zhang 2013; Sun et al. 2022a) also discussed this significant issue but without a straightforward conclusion.

The ambiguity in diagnostic characters poses a significant challenge to defining genera within the "*Biwia–Microphysogobio*" complex. This is evidenced by conflicting generic assignments for some species across previous studies (e.g., Bănărescu and Nalbant 1966; Yue 1998; Huang et al. 2016; Xu et al. 2016; He et al. 2017; Fricke et al. 2024), resulting from varying emphasis on genus characteristics derived from the type species. To resolve this taxonomic uncertainty, comprehensive diagnoses and an identification key for the genera within this complex are critically needed.

This study examines the type species of the four genera and includes a variety of species in the *Biwia–Microphysogobio* complex. Additionally, to comprehensively elucidate the phylogenetic relationships and taxonomic status of these genera, we conduct phylogenetic analyses of mitochondrial genome data. Supported by morphological and molecular evidence, new genera are established in this study. Each genus has been revised, accompanied by a list of valid species. A practical key to genera is also provided.

Materials and methods

Specimen collection, preservation, and examination

The specimens examined in this study were collected by hand nets, fish traps, or directly acquired from local fishermen. The field collections followed the "Implementation rules of Fisheries Law of the People's Republic of China" and the "Guide to Collection, Preservation, Identification and Information Share of Animal Specimens" (Xue 2010). The specimens used for morphological study were first fixed in 10% formalin solution for 3 days, then placed in clear water to remove formaldehyde, and ultimately preserved in 70% ethanol for long-term storage. The specimens or tissues used for molecular study were fixed in 95% ethanol. The type specimens and other vouchers examined are deposited at different museums, universities, and institutions as follows: Institute of Zoology, Chinese Academy of Sciences, Beijing, China (**ASIZB**); Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China (**IHB**); Biodiversity Research Museum, Biodiversity Research Center, Academia Sinica, Taipei, China (**ASIZP**); American Museum of Natural History, New York, United States (**AMNH**); National Museum of Nature and Science, Tokyo, Japan (**NSMT-P**); Kinki University, Nara, Japan (**KUN-P**); Laboratory of Ichthyology, Shanghai Ocean University, Shanghai, China (**SHOU**); National Taiwan Ocean University, Keelung, China (**NTOUP**); Freshwater Fisheries Research Institute of Jiangsu Province, Nanjing, China (**JS**); Zoological Museum of Fudan University, Shanghai, China (**FDZM**); South China Agricultural University, Guangzhou, China (**SCAU**). The institutional abbreviations follow the codes in Leviton et al. (1985). The comparative materials are listed in Suppl. material 1.

Morphological analyses

The measurements were taken point-to-point with a digital caliper accurate to 0.01 mm, and all measurements and counts were made on the left side of specimens. Photographs of the lip papillae system were first taken with a Nikon D600 camera with a 60 mm fixed-focus lens on a light background with a ruler for scale. The photographs were then measured with ImageJ v.1.52. Once the scale was specified, the distance between two points was measured with a straight line. The air bladders were also measured. Specimens of different sizes and sexes were dissected; the visceral mass was removed to expose the air bladder. The measurements of the air bladder are shown in Fig. 1. Other detailed methods of measurement and counts followed Sun et al. (2021).

Molecular phylogenetic analyses

Molecular phylogenetic analyses were based on mitochondrial genome sequences. DNA was extracted from the pelvic fin on the right side of specimens preserved in 95% ethanol using an SDS-based extraction combined with a purification column method. Once DNA tests were qualified, the samples were randomly fragmented

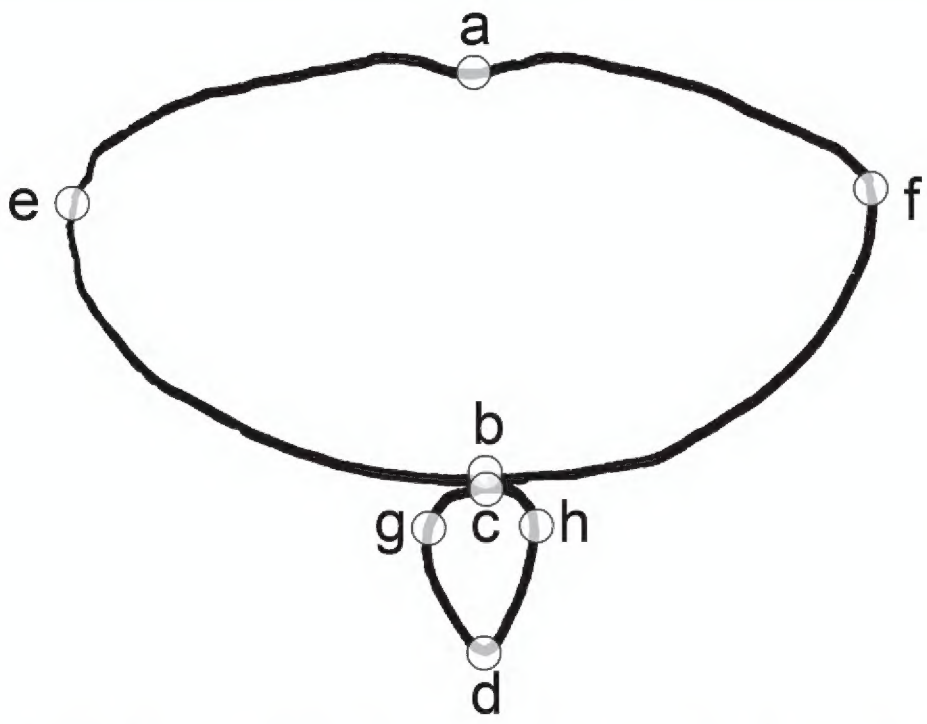

Figure 1. Illustration of morphometric measurements for air bladder comparison. Total air bladder length (**a–d**): the distance from the proximal margin of the anterior chamber to the distal margin of the posterior chamber. Anterior chamber length (**a–b**): the distance from the proximal margin of the anterior chamber to the distal margin. Anterior chamber width (**e–f**): the maximum horizontal width of the anterior chamber. Posterior chamber length (**c–d**): the distance from the proximal margin of the posterior chamber to the distal margin. Posterior chamber width (**g–h**): the maximum horizontal width of the posterior chamber.

using a Bioruptor Pico System (Diagenode, Belgium). Library preparation was then performed through steps including end repair, A-tailing, purification, and PCR amplification. The library preparation was conducted using the TrueLib DNA Library Rapid Prep Kit for Illumina (ABclonal Technology, China). Library preparation and genomic DNA sequencing (Next Generation Sequencing method) were performed at Beijing TSINGKE Biotech Co., Ltd. (China). The sequencing depth was 6×, and approximately 6 Gb of raw data were generated from each specimen. The raw data, together with a reference mitochondrial genome sequence (KJ933414) obtained from the National Center for Biotechnology Information (NCBI), were then used for data assembly with the Burrows–Wheeler Alignment Tool (Li and Durbin 2009). The mapped data, after unmatched parts were deleted, were converted to "bam" format from "sam" format using Samtools (Li et al. 2009). The "bam" files were transferred to Fastq files using BEDtools (Quinlan and Hall 2010). The paired-end sequences were assembled using Megahit (Li et al. 2015) and finally annotated with MitoFinder (Allio et al. 2020). The complete mitochondrial genome sequences of 11 species from the *Biwia–Microphysogobio* complex generated in this study and 36 sequences obtained from NCBI were included in the molecular phylogenetic analyses. Detailed information on sequences is shown in Table 1.

The complete mitochondrial genome sequences, including all tRNAs and the D-loop region, were used for analyses. Nucleotide sequence alignment was conducted with MAFFT v.7.313 (Katoh and Standley 2013). The dataset length after alignment was 16,715 bp. ModelFinder v.2.2.0 (Kalyaanamoorthy et al. 2017) was used to select the best-fit model under the Bayesian information criterion (BIC). The Bayesian inference (BI) phylogenies were inferred with MrBayes v.3.2.6 (Ronquist et al. 2012) under the GTR+F+I+G4 model (two parallel runs, 1,000,000 generations), with the initial 25% of sampled data discarded as burn-in. Convergence of the runs was assessed by the average standard deviation of split frequencies (less than 0.01) using MrBayes v.3.2.6. Maximum likelihood (ML) phylogenetic analysis was conducted with IQ-TREE v.2.2.0 (Nguyen et al. 2015) under the GTR+I+G model with 1000 ultrafast bootstraps (Minh et al. 2013). Trees were visualized with TVBOT (https://www.chiplot.online/tvbot.html; Xie et al. 2023).

Table 1. NCBI accession numbers of the mitochondrial genome sequences, sampling localities, and voucher codes of species in the *Biwia–Microphysogobio* complex and outgroup for molecular analyses.

Genus (Lineage)	Accession no.	Sequences length / bp	Species	Locality	Drainage	Voucher Code	Source
Platysmacheilus (Lineage I)	–	16613	*Pl. exiguus*	Chaling, Hunan, China	Middle Yangtze River basin	ASIZB 218804	This study
	KU314692	16615	*Pl. longibarbatus*	Ningdu, Jiangxi, China	Middle Yangtze River basin	FDZM-PLND20111101	Li et al. 2018
Crossocheilogobio (Lineage II)	KF857260	16605	*Mi. tafangensis*	Unknown	Unknown	–	Wang et al. 2014
	–	16606	*Mi. tafangensis*	Longquan, Zhejiang, China	Qiantangjiang River basin	ASIZB 218806	This study
Mesophysogobio (Lineage III)	ON357712	16614	*Mi. kachekensis*	Qionghai, Hainan, China	Wanquanhe River basin	–	Yang and Fu (Direct Submission)
	ON357713	16612	*Mi. kachekensis*	Baisha, Hainan, China	Nandujiang River basin	–	Yang and Fu (Direct Submission)
	–	16612	*Mi. kachekensis*	Baisha, Hainan, China	Nandujiang River basin	ASIZB 248165	This study
	ON357715	16611	*Mi. luhensis*	Luhe, Guangdong, China	Rongjiang River	–	Yang and Fu (Direct Submission)
	ON357716	16613	*Mi. bicolor*	Fuliang, Jiangxi, China	Middle Yangtze River basin	–	Yang and Fu (Direct Submission)
	–	16614	*Mi. bicolor*	Yanshan, Jiangxi, China	Middle Yangtze River basin	ASIZB 220619	This study

Genus (Lineage)	Accession no.	Sequences length / bp	Species	Locality	Drainage	Voucher Code	Source
Huigobio (Lineage IV)	KU314694	16610	*H. chenhsienensis*	Ningdu, Jiangxi, China	Middle Yangtze River basin	FDZM-HCND20111101	Li et al. 2018
	–	16601	*H. chenhsienensis*	Shengzhou, Zhejiang, China	Cao'ejiang River basin	ASIZB 218813	This study
	–	16592	*H. exilicauda*	Shixing, Guangdong, China	Beijiang River, Pearl River basin	ASIZB 218784	This study
	ON316825	16603	*H. heterocheilus*	Yanling, Hunan, China	Middle Yangtze River basin	–	Yang et al. 2022
Oriengobio (Lineage V)	–	16607	*Mi. pseudoelongatus*	Du'an, Guangxi, China	Xijiang River, Pearl River basin	ASIZB 248162	This study
	KJ933414	16600	*Mi. fukiensis*	Fujian, China	Minjiang River basin	–	Yang et al. 2014
	MN970213	16627	*Mi. tungtingensis*	Shibin, Guizhou, China	Middle Yangtze River basin	–	Luo et al. 2020
	–	16607	*Mi. tungtingensis*	Yangshuo, Guangxi, China	Xijiang River, Pearl River basin	ASIZB 240553	This study
	MG797640	16603	*Mi. kiatingensis*	Chengdu, Sichuan, China	Upper Yangtze River basin	20170925BB05	Zou et al. 2018
	–	16605	*Mi. vietnamica*	Shixing, Guangdong, China	Beijiang River, Pearl River basin	ASIZB 240568	This study
	–	16607	*Mi. microstomus*	Shaoxing, Zhejiang, China	Cao'ejiang River system	ASIZB-SX01ZJ	This study
	–	16615	*Mi. zhangi*	Pingle, Guangxi, China	Xijiang River, Pearl River basin	ASIZB-PLLJ02GX	This study
	KC762939	16568	*Mi. alticorpus*	Unknown	Unknown	–	Lin et al. 2013
Biwia (Lineage VI)	AB250107	16599	*B. zezera*	Gifu, Japan	Nagara River basin	–	Horikawa et al. 2007
	ON357689	16598	*B. yodoensis*	Seika, Kyoto, Japan	Yodo River basin	–	Yang and Fu (Direct Submission)
Microphysogobio (Lineage VII)	AP011360	16606	*B. springeri*	Unknown	Unknown	CBM-ZF-11346	Tang et al. 2011
	AP011394	16603	*Mi. longidorsalis*	Unknown	Unknown	CBM-ZF-11551	Tang et al. 2011
	FJ515920	16606	*Mi. koreensis*	South Korea	Unknown	–	Hwang et al. 2013
	–	16600	*Mi. hsinglungshanensis*	Xinglong, Hebei, China	Luanhe River basin	ASIZB 248160	This study
	–	16602	*Mi. chinssuensis*	Yichuan, Henan, China	Middle Yellow River baisn	ASIZB 248161	This study
	KF319122	16608	*Mi. brevirostris*	Taiwan, China	Unknown	–	Wu (Direct Submission)
	ON357694	16610	*Mi. oujiangensis*	Fu'an, Fujian, China	Jiaoxi River	–	Yang and Fu (Direct Submission)
	KP677283	16607	*Mi. xianyouensis*	Xianyou, Fujian, China	Mulanxi River	–	Zhou and Chen (Direct Submission)
	KR075133	16601	*Mi. yaluensis*	Unknown	Unknown	–	Park et al. (Direct Submission)
	MH713708	16603	*Mi. rapidus*	South Korea	Unknown	–	Kim et al. (Direct Submission)
	MN581867	16602	*Mi. jeoni*	Buyeo, South Korea	Geum River	–	Kim et al. 2020
	KY228977	16605	*Mi. amurensis*	Heilongjiang, China	Lake Khanka, Amur River basin	SCAU 1179906	Chen and Li 2017
Outgroups							
Pseudogobio	NC013759	16609	*Ps. esocinus*	Yagi, Kyoto, Japan	Katsura River, Yodo River basin	–	Saitoh et al. 2011
	MN883564	16606	*Ps. guilinensis*	Pingle, Guangxi, China	Xijiang River, Pearl River basin	FDZM-PGuPingL20170716-01	Fu and Fu 2020
Abbottina	KM081703	16597	*A. rivularis*	Unknown	Unknown	–	Wang et al. 2016
	MK852690	16599	*A. rivularis*	Erguna, Inner Mongolia, China	Amur River basin	FDZM-ARER20170826	Chen and Fu 2019
Saurogobio	KU314696	16609	*S. dabryi*	Xiushui, Jiangxi, China	Middle Yangtze River basin	FDZM-SDXS20120401	Li et al. 2018
	KF151214	16601	*S. dumerili*	China	Unknown	–	Wan et al. 2015
Gobiobotia	KU314697	16605	*Gobiobitia pappenheimi*	Tieling, Liaoning, China	Liaohe River basin	FDZM-GPTL20110501	Li et al. 2018
Xenophysogobio	ON920186	16609	*X. boulengeri*	Luzhou, Sichuan, China	Upper Yangtze River basin	–	Li (Direct Submission)
Gobio	KU314700	16605	*Gobio cynocephalus*	Jalaid Banner, Nei Mongol, China	Amur River basin	FDZM-GCJAL20110701	Li et al. 2018
Hemibarbus	DQ347952	16608	*He. longirostris*	South Korea	Namhan River	–	Kim et al. 2009

Results

Molecular phylogenetic relationships

Mitochondrial genome sequences from 40 species are included in the molecular phylogenetic analyses in this study. Both Bayesian inference (BI) and maximum likelihood (ML) methods show a similar tree topology (Fig. 2), with the only difference being the position of the genus *Platysmacheilus*: it forms a sister group with the lineage comprising the other six lineages within the *Biwia–Microphysogobio* complex in the BI tree, while forming a sister group with the branch comprising Lineage II and Lineage III in the ML tree. In the BI tree (Fig. 2A), 34

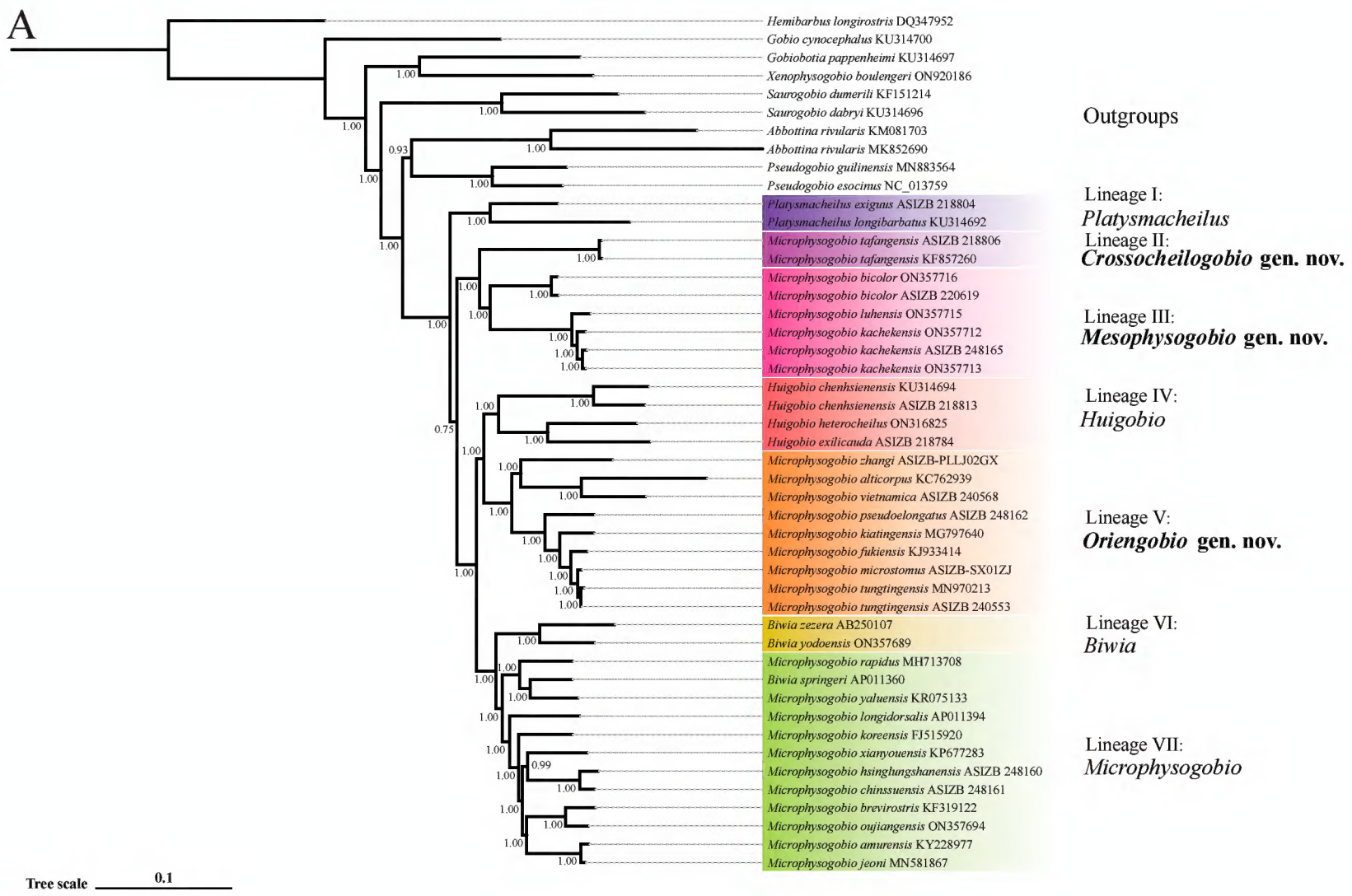

Figure 2. The phylogenetic relationship of seven genera within the *Biwia–Microphysogobio* complex. **A.** Bayesian inference (BI) tree, posterior probabilities shown at nodes; **B.** maximum likelihood (ML) tree, bootstrap values shown at nodes.

out of the 36 nodes within the ingroup possess posterior probabilities of 1.00, one node has posterior probabilities greater than 0.90 (0.99), and one node has posterior probabilities of 0.75. Each genus in the BI tree shows a monophyletic nature. In the ML tree (Fig. 2B), 31 out of 36 nodes within the ingroup have bootstrap values higher than 90. Relatively low bootstrap values are present within one lineage (e.g., the branch including ON357712, ASIZB 248165, and ON357713). In addition, another low bootstrap value (0.55) is present at the node between the genus *Platysmacheilus* and the branch consisting of Lineage II and Lineage III. All genera in the ML tree are resolved as monophyletic.

The phylogenetic relationships inferred using the BI method (Fig. 2A) based on mitochondrial genome sequences within the *Biwia–Microphysogobio* complex can be summarized as follows: (1) the complex is formed by three major groups: a group consisting of *Platysmacheilus*, a group consisting of Lineages II and III, and a group consisting of *Huigobio*, Lineage V, *Biwia*, and *Microphysogobio*; (2) *Platysmacheilus* is the sister group to the other two groups, while the latter two groups form sister groups with each other; (3) Lineage II is the sister group to Lineage III; (4) the latter group is comprised of two sister-group pairs, one consisting of *Biwia* and *Microphysogobio* and the other consisting of *Huigobio* and Lineage V; (5) the type species of each genus is placed within its respective genus.

The phylogenetic relationships inferred using the ML method (Fig. 2B) based on mitochondrial genome sequences within the *Biwia–Microphysogobio* complex can be summarized as follows: (1) the complex is formed by two major groups, one consisting of *Platysmacheilus*, Lineage II, and Lineage III, and the other consisting of *Huigobio*, Lineage V, *Biwia*, and *Microphysogobio*; (2) within the former group, Lineage II and Lineage III form a sister group, and these two lineages form the sister group to *Platysmacheilus*; (3) the latter group is comprised of two sister-group pairs, one consisting of *Biwia* and *Microphysogobio* and the other consisting of *Huigobio* and Lineage V; (4) the type species of each genus is placed within its respective genus.

Generic-level characters

Upper jaw horny margin

Apart from the genus *Biwia*, which possesses an insignificant upper jaw horny margin (Fig. 3A), the upper jaw can be categorized into three major types. Type A, wide, and usually larger than half of the mouth width, includes two lineages: *Microphysogobio* and *Huigobio*. The upper jaw margin width as a percentage of mouth width ranges from 50.2%–70.4% (means from eight species, Table 2) in *Microphysogobio* (Fig. 3B), and 66.8%–73.3% (means from three species, Table 2) in *Huigobio* (Fig. 3C). Type B, narrow, usually smaller than half but larger than one quarter of the mouth width, includes three lineages: *Platysmacheilus*, Lineage III, and Lineage V. The upper jaw margin width as a percentage of mouth width ranges from

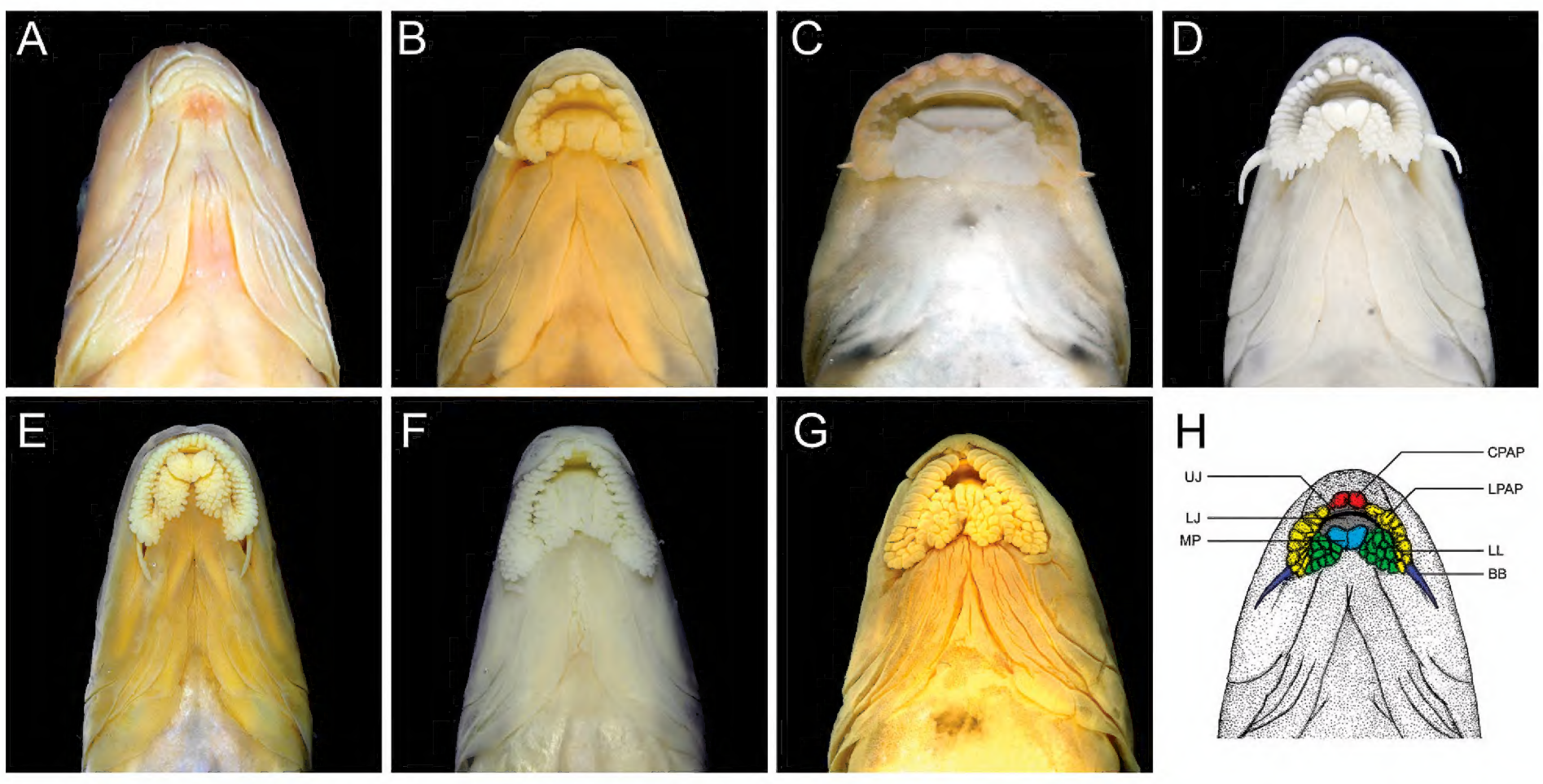

Figure 3. Lip papillae patterns of the type species of seven genera within the *Biwia–Microphysogobio* complex, with a diagrammatic illustration showing the structures. **A.** *Biwia zezera*, KUN-P040282; **B.** *Microphysogobio hsinglungshanensis*, ASIZB 240788; **C.** *Huigobio chenhsienensis*, SHOU 20231209015; **D.** *Oriengobio fukiensis*, ASIZB 220659; **E.** *Mesophysogobio kachekensis*, ASIZB 69768; **F.** *Platysmacheilus exiguus*, ASIZB 220879; **G.** *Crossocheilogobio tafangensis*, ASIZB 60212; **H.** diagrammatic illustration based on *Microphysogobio chinssuensis*. CPAP = central portion of anterior papillae; LPAP = lateral portion of anterior papillae; MP = medial pad; LL = lateral lobe; BB = barbel; UJ = upper jaw; LJ = lower jaw. The photo of *Biwia zezera* is provided by Seigo Kawase; the other photos and illustration were made by Zhi-Xian Sun.

Table 2. Morphometric measurements of the seven genera of the *Biwia–Microphysogobio* complex, with a brief summary of each characteristic. "N" in the table indicates the number of individuals measured.

Genus	Species	Upper jaw width/Mouth width				Posterior chamber length/Eye diameter				Posterior chamber length/Anterior chamber length			
		Mean	Range	N	Summary	Mean	Range	N	Summary	Mean	Range	N	Summary
Biwia	*Biwia zezera*	NA	NA	1	NA	NA	NA	NA	>1/2 Eye Diameter	NA	NA	NA	Posterior>Anterior
Microphysogobio	*Mi. hsinglungshanensis*	70.1%	57.4%–81.1%	12	>1/2 Mouth Width	32.5%	26.3%–39.5%	4	<1/2 Eye Diameter	57.3%	40.3%–74.7%	4	Posterior<Anterior
	Mi. chinssuensis	70.4%	53.6%–89.6%	23		30.9%	26.1%–36.2%	3		71.0%	55.4%–85.2%	3	
	Mi. yaluensis	69.1%	60.0%–77.8%	15		25.6%	21.8%–33.3%	5		63.3%	50.3%–85.1%	5	
	Mi. nudiventris	64.4%	56.1%–75.3%	28		NA	NA	NA		NA	NA	NA	
	Mi. oujiangensis	50.2%	42.9%–55.5%	21		35.3%	NA	1		NA	NA	NA	
	Mi. brevirostris	68.1%	62.9%–77.3%	9		NA	NA	NA		NA	NA	NA	
	Mi. xianyouensis	61.0%	54.1%–74.0%	9		NA	NA	NA		NA	NA	NA	
	Mi. amurensis	61.0%	59.2%–62.6%	3		NA	NA	NA		NA	NA	NA	
Huigobio	*H. chenhsienensis*	73.3%	65.2%–77.6%	9	>1/2 Mouth Width	27.1%	24.1%–31.5%	4	<1/2 Eye Diameter	47.8%	37.6%–62.7%	4	Posterior<Anterior
	H. exilicauda	69.7%	63.8%–73.8%	15		24.3%	19.8%–26.2%	5		66.8%	60.3%–74.3%	5	
	H. heterocheilus	66.8%	59.0%–71.2%	15		NA	NA	NA		NA	NA	NA	
Oriengobio gen. nov.	*O. fukiensis*	34.4%	25.0%–39.4%	20	<1/2 Mouth Width	27.7%	19.4%–42.2%	6	usually <1/2 Eye Diameter	57.0%	43.0%–79.1%	6	usually Posterior<Anterior
	O. tungtingensis	28.8%	17.8%–43.2%	37		33.2%	29.0%–38.4%	9		76.7%	62.2%–91.6%	9	
	O. pseudoelongatus	35.3%	25.7%–47.1%	9		45.8%	NA	1		100.5%	NA	1	
	O. microstomus	30.9%	26.6%–39.6%	16		84.3%	70.4%–93.7%	5		173.7%	127.3%–220.8%	5	
	O. vietnamica	35.4%	27.4%–44.9%	12		48.1%	35.5%–64.2%	10		NA	NA	NA	
	O. zhangi	34.5%	22.5%–47.1%	19		32.4%	24.0%–41.3%	4		63.9%	49.0%–78.6%	4	
	O. kiatingensis	31.4%	22.4%–40.8%	13		NA	NA	NA		NA	NA	NA	
Mesophysogobio gen. nov.	*Me. kachekensis*	28.2%	20.0%–34.5%	22	<1/2 Mouth Width	88.0%	60.9%–101.1%	9	>1/2 Eye Diameter	180.6%	115.6%–220.5%	9	Posterior>Anterior
	Me. yunnanensis	33.6%	25.0%–40.3%	12		97.4%	56.1%–114.2%	7		NA	NA	NA	
	Me. luhensis	39.1%	NA	1		NA	NA	NA		NA	NA	NA	
	Me. bicolor	33.9%	25.4%–51.5%	22		82.0%	NA	1		NA	NA	NA	
	Me. punctatus	39.1%	31.1%–46.8%	41		68.2%	50.3%–82.8%	12		157.7%	84.2%–235.5%	9	
Platysmacheilus	*P. exiguus*	32.4%	28.3%–34.4%	5	<1/2 Mouth Width	29.1%	27.0%–31.3%	2	<1/2 Eye Diameter	66.9%	64.5%–69.3%	2	Posterior<Anterior
	P. longibarbatus	35.1%	33.0%–37.7%	3		NA	NA	NA		NA	NA	NA	
Crossocheilogobio gen. nov.	*C. tafangensis*	23.1%	16.6%–27.5%	15	≈1/4 Mouth Width	32.5%	30.7%–36.5%	4	<1/2 Eye Diameter	60.9%	49.0%–73.4%	4	Posterior<Anterior

25.8%–35.4% (means from seven species, Table 2) in Lineage V (Fig. 3D), 28.2%–39.1% (means from five species, Table 2) in Lineage III (Fig. 3E), and 32.4%–35.1% (means from two species, Table 2) in *Platysmacheilus* (Fig. 3F). Type C, extremely narrow, approximately equal to one quarter of the mouth width, includes Lineage II. The upper jaw margin width as a percentage of mouth width is 23.1% (range 16.6%–27.5%, Table 2; Fig. 3G).

Central portion of the anterior papillae

Central portion of the anterior papillae row numbers are distinguishable amongst genera. The genus *Microphysogobio*, Lineage II, Lineage III, and Lineage V have only one row (Fig. 3B, D, E, G). The genera *Huigobio* and *Platysmacheilus* have two or more rows, and extra rows are usually hidden underneath the first

row (Fig. 3C, F). The genus *Biwia* has no papillae on the upper lip (Fig. 3A).

The central portion of the anterior papillae size and shape can be categorized into two types. The first type shows a pair of enlarged papillae, which are usually obvious to recognize. The genera *Microphysogobio*, *Huigobio*, Lineage II, and Lineage V belong to this type. The second type shows not significantly enlarged papillae, and the pair is not easily or not able to be recognized since they are tightly contacted. These papillae are usually the same size as the papillae on the lateral portion of the upper lip. Lineage III and the genus *Platysmacheilus* belong to this type.

Air bladder

The size of the air bladder is another diagnostic character for genus differentiation, particularly in identifying the genus *Biwia* and Lineage III from the other five lineages. The genera *Microphysogobio*, *Huigobio*, *Platysmacheilus*, and Lineage II have the tiny and thin posterior chamber of the air bladder (Fig. 4A). The length of the posterior chamber is usually shorter than the anterior chamber length: 57.3%–71.0% (range of means concluded from three species, Table 2) in *Microphysogobio*; 47.8%–66.8% (range of means concluded from two species, Table 2) in *Huigobio*; 66.9% (range 64.5%–69.3%

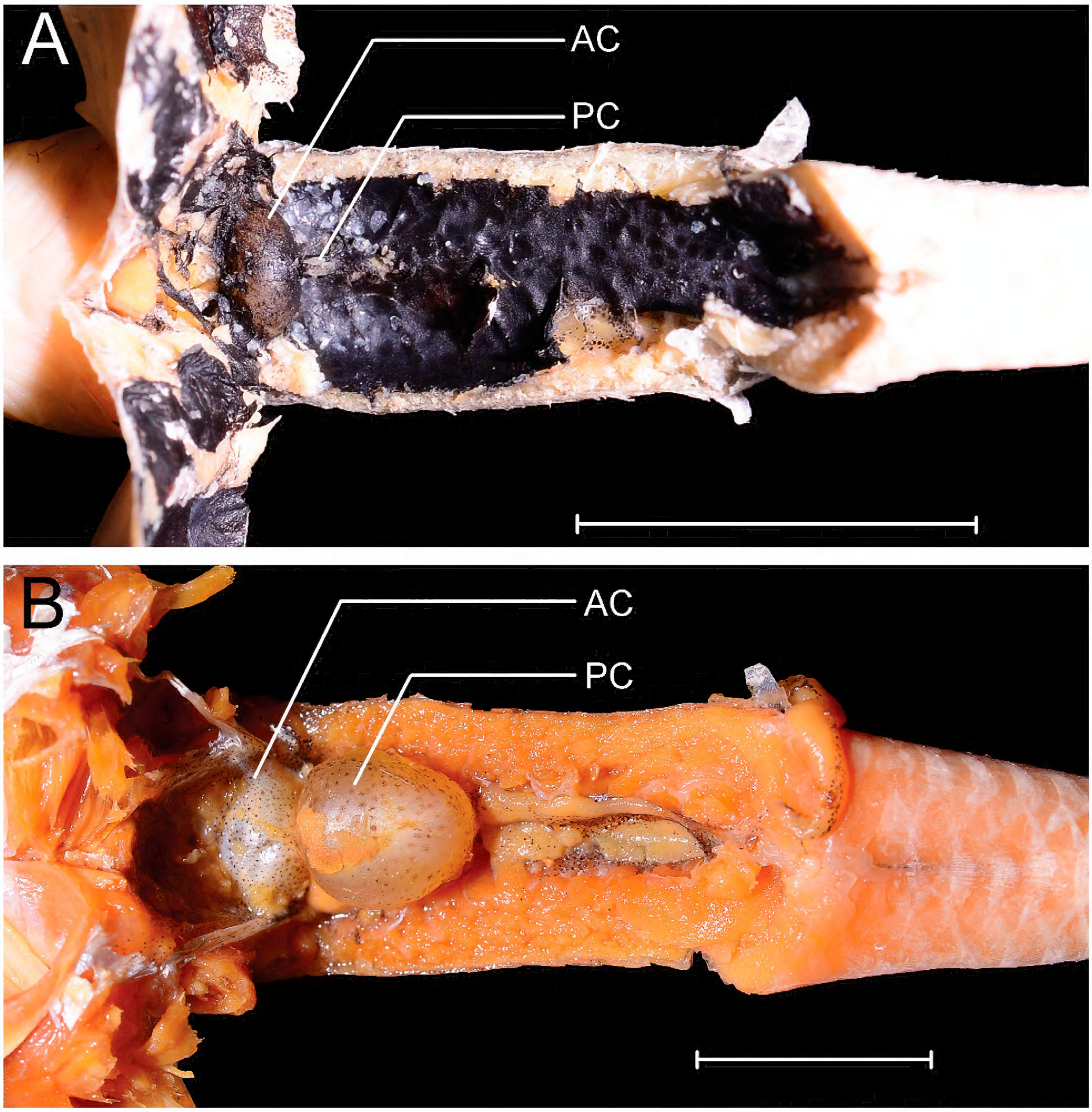

Figure 4. The air bladder apparatus of the genera *Microphysogobio* and *Mesophysogobio* gen. nov. **A.** *Microphysogobio hsinglungshanensis*, ASIZB 247945; **B.** *Mesophysogobio kachekensis*, ASIZB 240478. AC = anterior chamber; PC = posterior chamber. Scale bar: 10 mm.

in *P. exiguus*) in *Platysmacheilus*; and 60.9% (range 49.0%–73.4%) in Lineage II. Lineage V also has the small posterior chamber, 57.0%–76.7% (range of means concluded from 3 species, Table 2), with the exceptions of *Microphysogobio pseudoelongatus* (100.5% of anterior chamber length) and *M. microstomus* (127.3%–220.8% of anterior chamber length). *Biwia* and Lineage III are two lineages having relatively enlarged posterior chambers. The air bladder morphology of *Biwia* followed Kawase (2014), with the posterior chamber rounded and larger than the anterior chamber. The length of the posterior chamber is usually longer than the anterior chamber length in Lineage III (157.7%–180.6%, range of means concluded from two species, Table 2; Fig. 4B). The relative proportions between the posterior chamber and eye diameter are also shown in Table 2. The genera *Microphysogobio*, *Huigobio*, *Platysmacheilus*, Lineage II, and Lineage V have the posterior chamber length less than half of the eye diameter, while *Biwia* and Lineage III are larger than half of the eye diameter.

Discussion

Previous studies suggested that the phylogenetic placement of *Biwia* and *Huigobio* disrupts the monophyly of *Microphysogobio* (e.g., Tang et al. 2011; Li et al. 2018; Chen et al. 2023). The genus *Biwia*, endemic to Japan, is the first genus established within the *Biwia–Microphysogobio* complex (Jordan and Fowler 1903). This genus is located at a relatively terminal position in the phylogenetic trees (Li et al. 2018; Chen et al. 2023; the same in this study). The genus *Microphysogobio*, widely distributed in mainland East Asia, was established later in 1934. Although *Biwia* and *Microphysogobio* are sister groups, we recognize both genera as valid because of the unique morphological characters of *Biwia*: no barbel, relatively simple and less developed lips, and an enlarged posterior chamber of the air bladder (Kawase and Hosoya 2010; Kawase 2014). In other words, the genus characters of *Biwia* do not adequately represent those species within *Microphysogobio*. The reasons above destined the previous "*Microphysogobio*" as a non-monophyletic genus, and this is also the major issue previous taxonomic studies faced. Therefore, we describe three new genera that contain species that were previously treated as species of *Microphysogobio*. A comprehensive taxonomic revision of the *Biwia–Microphysogobio* complex in this study renders all seven genera, with their type species included, monophyletic (Fig. 2). Keys and detailed descriptions of these seven genera are provided in the Taxonomy revision.

The topologies of molecular phylogenetic trees in this study are similar to the recent molecular phylogenetic study (Chen et al. 2023). Both studies show that *Huigobio* is sister to the lineage represented by *Microphysogobio fukiensis* (i.e., Lineage V in this study), and *Biwia* is sister to the lineage consisting of the species belonging to *Microphysogobio sensu stricto*. This study includes five sequences forming Lineage III, which were not included by Chen et al. (2023). However, the position of *Microphysogobio tafangensis* (i.e., Lineage II in this study) is similar, forming a sister group with the group comprising *Biwia*, *Microphysogobio*, *Huigobio*, and Lineage V. Since the data source of the species in the genus *Platysmacheilus* is unclear, we choose to use the sequences that have the correct identity. Although the lineage of the genus *Platysmacheilus* has different positions in BI and ML methods, the monophyletic nature of each genus still remains. Thus, the molecular phylogenetic relationships are relatively stable, and this result is treated as important evidence supporting the generic differentiation in this study.

Among these seven lineages, only Lineage V exhibits an exception: *Microphysogobio alticorpus* does not conform to the diagnostic morphological characteristics of Lineage V. It possesses a wide upper jaw horny margin that is larger than half of the mouth width (Sun et al. 2022b). We thus maintain the current taxonomic status of this species in the genus *Microphysogobio* primarily based on its morphological congruence with this genus. The potential causes of this discordance between molecular phylogenies and morphological classification may arise from two possible methodological or biological sources: (1) long-branch attraction (LBA). In both this and prior studies (Sun and Zhao 2022; Sun et al. 2022b, 2024), this species exhibits a long branch in mitochondrial phylogenies, suggesting potential analytical artifacts (e.g., LBA; Felsenstein 1978) that may yield inaccurate topology; and (2) mitochondrial introgression. This species could be a *Microphysogobio* species carrying the mitochondrial genome of an ancestral species in Lineage V, and a similar case has also been found in other freshwater fish species (e.g., *Nothonotus camurus*; Stokes et al. 2023). Due to the lack of nuclear gene sequences for *M. alticorpus* in public databases (i.e., NCBI) and the unavailability of specimens for molecular study, this study restricts current findings to mitochondrial genome-based reconstructions. Resolving the phylogenetic incongruence observed in *M. alticorpus* should be addressed in future studies by incorporating nuclear genomic data.

The *Biwia–Microphysogobio* complex is distributed only in the Russian Far East, eastern Mongolia, southern and eastern China, the Korean Peninsula, the Kyushu and Honshu islands of Japan, northern Vietnam, and northern Laos (Fig. 5A). Among the seven genera, *Biwia* is the only genus not distributed in mainland East Asia. It is restricted to northern Kyushu and southern Honshu of Japan (Fig. 5B). The other six genera are distributed in rivers in mainland East Asia that drain to the Pacific Ocean. The genus *Microphysogobio* has the broadest distribution among these genera, from the Amur River Basin at the border of Russia, China, and Mongolia to the southeast coastal rivers of China (Fig. 5C). Most of the *Microphysogobio* species (ca. 13) are distributed north of

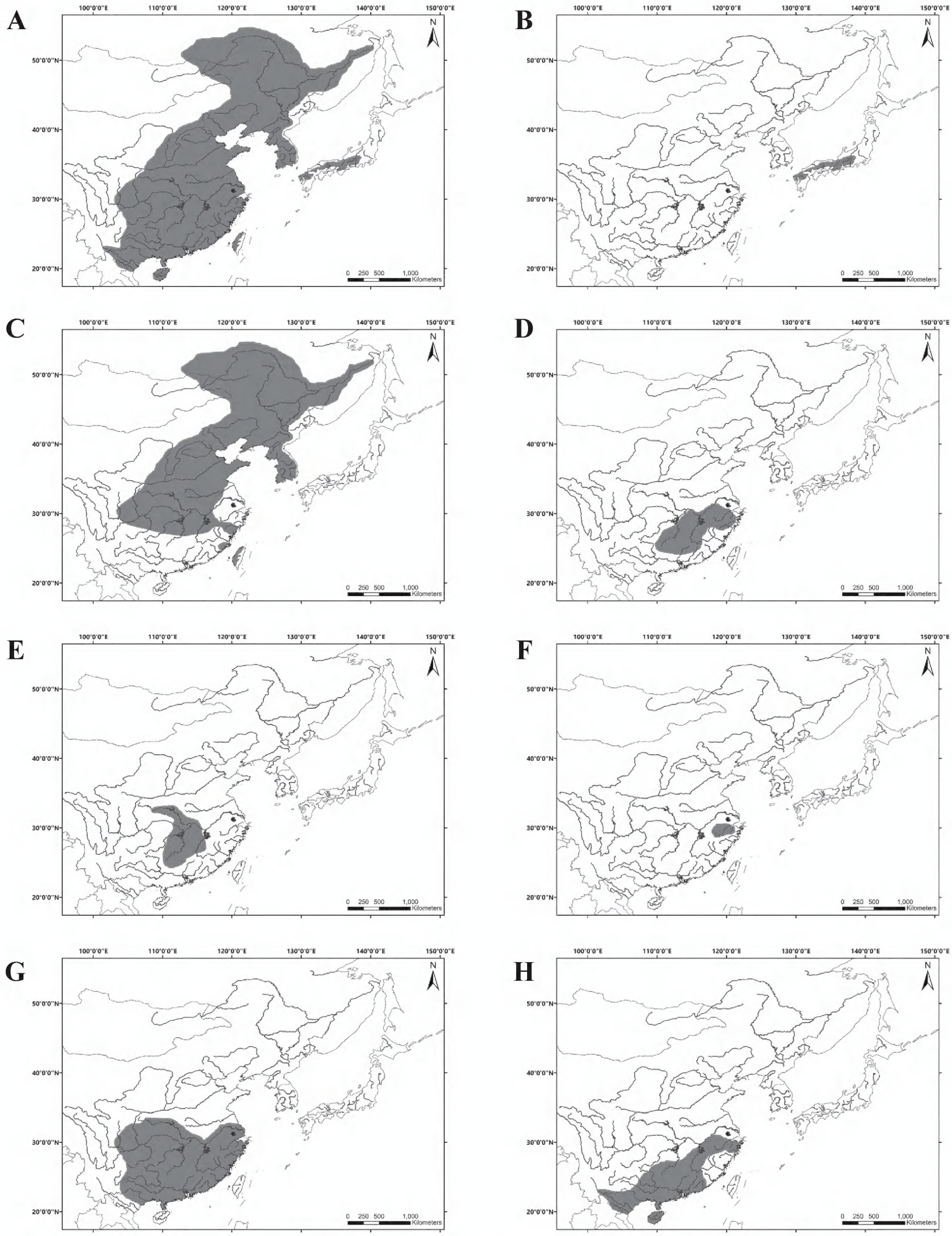

Figure 5. The distributions of the *Biwia–Microphysogobio* complex and seven genera. **A.** The complex; **B.** *Biwia*; **C.** *Microphysogobio*; **D.** *Huigobio*; **E.** *Platysmacheilus*; **F.** *Crossocheilogobio* gen. nov.; **G.** *Oriengobio* gen. nov.; **H.** *Mesophysogobio* gen. nov.

the Yangtze River Basin, two valid species are distributed in the Yangtze River Basin, and four valid species are distributed in the coastal rivers of southeast China. Lineage II, *Huigobio*, and *Platysmacheilus* are endemic to southern China. Among them, the genera *Huigobio* and *Platysmacheilus* have broader distribution areas (Fig. 5D, E), while Lineage II is currently known mainly in the Qiantangjiang River Basin (Fig. 5F). The remaining two

genera are mainly distributed in southern China and also northern Vietnam. All nine valid species of Lineage V are distributed south of the Yangtze River Basin (including the Yangtze River). The southernmost species are *M. vietnamica* and *M. pseudoelongatus*, distributed in China and Vietnam (Fig. 5G). The distribution of Lineage III is similar to Lineage V but excludes the upper Yangtze River and some coastal rivers (e.g., the Oujiang and Minjiang Rivers) in Zhejiang and Fujian Provinces (Fig. 5H). It is further distributed in the Red River Basin in northern Vietnam and the Ma River Basin in northern Laos, and *M. yunnanensis* should be the southernmost species of this lineage. This comprehensive distribution pattern not only supports the current generic revision but also provides valuable insights into the evolutionary radiation of the *Biwia–Microphysogobio* complex.

Taxonomy revision

Key to the seven genera in the *Biwia-Microphysogobio* complex

1a Barbel absent ..... *Biwia* Jordan & Fowler, 1903 (Japan)
– Barbel present 2
2a Horny margin on upper jaw wide, width larger than half mouth width 3
– Horny margin on upper jaw narrow, width smaller than half mouth width 4
3a Central portion of anterior papillae on upper lip in one row, lateral lobes on lower lip not in contact behind medial pad ..... *Microphysogobio* Mori, 1934 (China, Russian Far East, eastern Mongolia, and Korean Peninsula)
– Central portion of anterior papillae on upper lip more than one row, lateral lobes on lower lip contact with each other behind medial pad, or medial pad fused with lateral lobes ..... *Huigobio* Fang, 1938 (southern China)
4a Posterior chamber of the air bladder length larger than half eye diameter, equal to or slightly larger than anterior chamber, lower jaw not exposed, covered by medial pad ..... *Mesophysogobio* gen. nov. (southern China, northern Vietnam, and northern Laos)
– Posterior chamber of the air bladder length smaller than half eye diameter, smaller than anterior chamber 5
5a Central portion of anterior papillae on upper lips more than one row, lobes on lower lip formed together, with a notch in anterior of the lower lip ..... *Platysmacheilus* Lo, Yao & Chen, 1977 (southern China)
– Central portion of anterior papillae on upper lip in one row 6
6a Central portion of anterior papillae on upper lip enlarged, not covered by rostral cap, lower jaw exposed from medial pad ..... *Oriengobio* gen. nov. (southern China, northern Vietnam)
– Central portion of anterior papillae on upper lip with two papillae, semi-covered by rostral cap, medial pad on lower lip possessing two elongated thin protrusions, lower jaw exposed from medial pad ..... *Crossocheilogobio* gen. nov. (southern China)

Biwia Jordan & Fowler, 1903

Fig. 6

Biwia Jordan & Fowler, 1903: 838. Type species: *Pseudogobio zezera* Ishikawa, 1895.

Diagnosis. The genus *Biwia* can be distinguished from the other genera within the Pseudogobionini by having no barbel.

Description. Body elongated, rather rounded, laterally compressed, and somewhat broad forward. Mouth arc-shaped and inferior; no barbel; lips thin, smooth, no papillae; lower lip possessing two rounded fleshy protrusion, smooth, without papillae, forming the medial pad; lower lip connected with each other anterior from medial pad and laterally connected with upper lip around mouth corners (Fig. 3A). Body covered with moderately large cycloid scales. Thoracic region scaleless. Anus positioned in anterior one-third of pelvic-fin insertion and anal-fin base. Lateral line complete, almost straight. Lateral-line scales usually 34–38; scales above lateral line 4.5; scales below lateral line usually 3; predorsal scales 10–11; circumpeduncular scales 12. Dorsal fin with three or four unbranched and six or seven branched rays, pectoral fin with one unbranched and nine or ten branched rays, pelvic fin usually with one unbranched and seven or eight branched rays, anal fin with three unbranched and six branched rays; caudal fin forked, with one simple ray and eight or nine branched rays on upper lobe, and seven or eight branched rays and one simple ray on lower lobe, lobes pointed. Pharyngeal teeth "5–5" in one row. Air bladder slightly enlarged, possessing two chambers; anterior chamber flat rounded, enclosed in a thick fibrous capsule; posterior chamber enlarged, length larger than anterior chamber length, spherical-shaped. Intestine short, simple.

Distribution. This genus distributed in northern Kyushu, Sanyo, the Yodo River Basin (including Lake Biwa), and the Nagoya Basin (Nobi Plain). This genus is endemic to Japan (Fig. 5B).

Etymology. The generic name refers to Lake Biwa, where the type species *Biwia zezera* occurs. The generic name in Chinese is "琵琶湖鮈"属, and the Chinese Pinyin name is "Pí Pa Hú Jū" Shǔ.

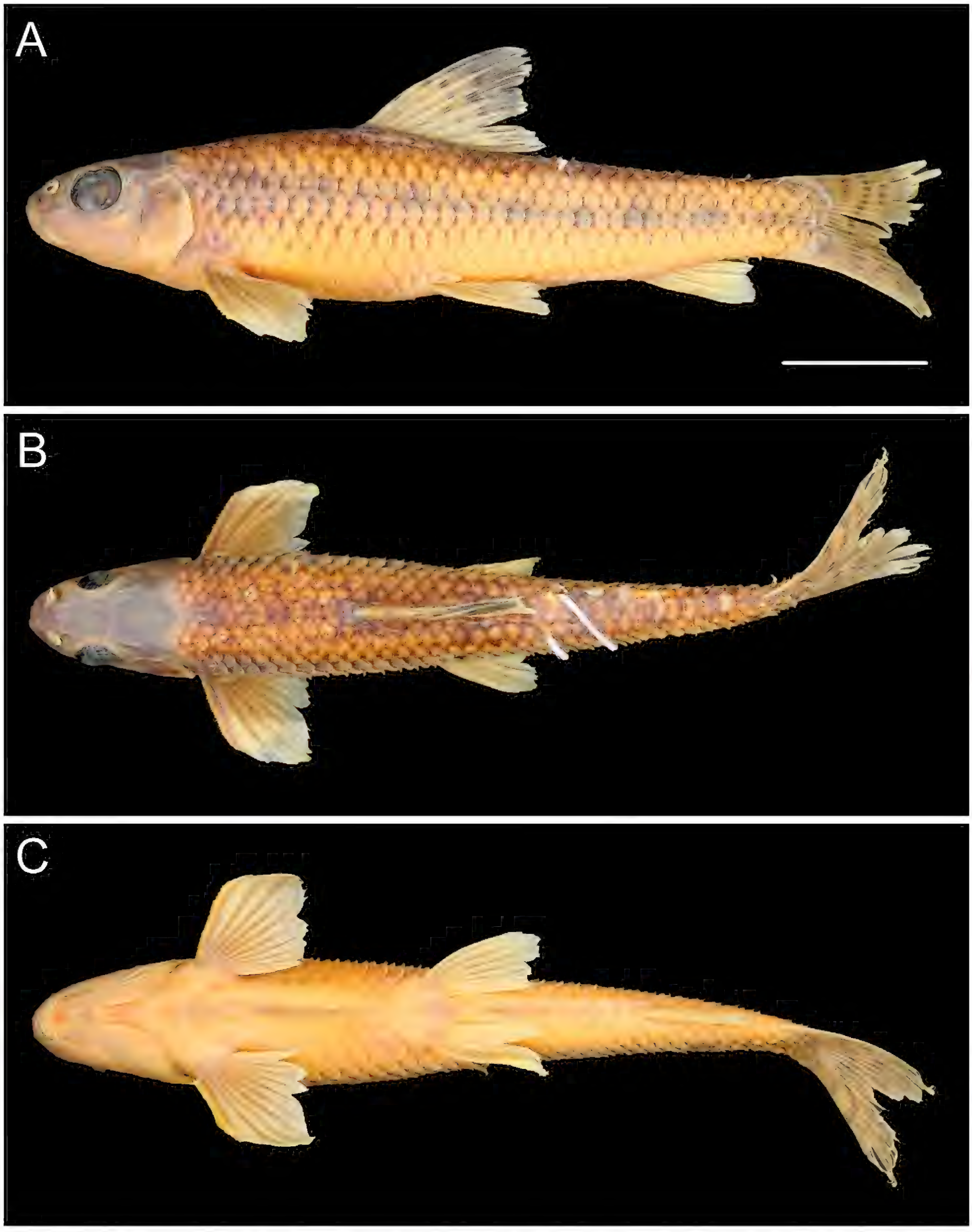

Figure 6. The general view of *Biwia zezera*, the type species of the genus *Biwia*, KUN-P 040282, male, 53.8 mm SL, collected from Lake Biwa, Moriyama, Shiga, Japan. **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view. Scale bar: 10 mm. Photographed by Seigo Kawase.

Species included.

Biwia zezera (Ishikawa, 1895) (type species).

Biwia yodoensis Kawase & Hosoya, 2010.

Remarks. This genus is restricted to only two valid species, *Biwia zezera* and *B. yodoensis*. *Biwia tama* Oshima, 1957, was described based on a single specimen collected from downstream of the Tama River in Denyencho-fu, Japan. According to the original description (Oshima 1957, Fig. 2), the holotype actually represents a *Sarcocheilichthys* species. *Biwia springeri* (Bănărescu & Nal-

bant, 1973), originally described as *Abbottina springeri* from Pusan, South Korea, does not have the characters of *Biwia*. Having one pair of barbels, an arc-shaped mouth, a wide horny-sheathed upper jaw, and a three-lobed lower lip, this species should be placed in *Microphysogobio*.

Microphysogobio Mori, 1934

Fig. 7

Microphysogobio Mori, 1934: 39. Type species: *Microphysogobio hsinglungshanensis* Mori, 1934.

Rostrogobio Taranetz, 1937: 114. Type species: *Rostrogobio amurensis* Taranetz, 1937.

Diagnosis. This genus can be distinguished from the other genera within the Pseudogobionini by the combination of the characters: (1) mouth arc-shaped and inferior; (2) central portion of the anterior papillae usually larger than lateral portion of anterior papillae on upper lip, in one row; (3) lower lip forming two lateral lobes and a medial pad, without anterior fold; (4) lateral lobes on lower lip not in contact with each other posteriorly from medial pad; (5) medial pad on lower lip heart-shaped or inverted trapezoid-shaped, sometimes bisected or grooved; (6) upper jaw wide, the horny margin width larger than half mouth width; (7) lower jaw exposed; (8) barbel in one pair; (9) midventral region of body scaleless or sometime covered with scales; (10) pharyngeal teeth in one row; (11) anterior chamber of the air bladder enclosed in thick fibrous capsule; (12) posterior chamber relatively small, length smaller than half eye diameter, smaller than anterior chamber length, thin.

Description. Body elongated, abdomen rounded; caudal peduncle short, compressed laterally. Mouth arc-shaped and inferior; barbel one pair; lips thick, with developed papillae; central portion of the anterior papillae usually larger than lateral portion of anterior papillae on upper lip, in one row, lateral portion of anterior papillae in several rows; lower lip forming two lateral lobes and one medial pad, without anterior fold; two lateral lobes on lower lip not in contact with each other posteriorly from medial pad, laterally connected with upper lip anterior papillae around mouth corners; medial pad on lower lip heart-shaped or inverted-trapezoidshaped, sometimes bisected or grooved. Upper and lower jaws with horny sheathed edge; upper jaw wide, horny margin width larger than half mouth width; lower jaw exposed (Fig. 3B). Body covered with moderately large cycloid scales. Thoracic region scaleless, mid-ventral region scaleless or covered with scales. Anus positioned in anterior one-third of pelvic-fin insertion and anal-fin base. Lateral line complete, almost straight. Lateral-line scales usually 35–40; scales above lateral line 3.5–5; scales below lateral line usually 1.5–2; predorsal scales 9–13; circumpeduncular scales 12. Distal margin of expanded dorsal fin steep sloped, usually slightly concave, with three unbranched and seven branched rays, pectoral fin with one unbranched and 10–12 branched rays, pelvic fin usually with one unbranched and six or seven branched rays, anal fin with three unbranched and six branched rays; caudal fin forked, with one simple ray and nine branched rays on upper lobe and eight branched rays and one simple ray on lower lobe, lobes pointed. Pharyngeal teeth "5–5" in one row. Air bladder small, possessing two chambers; anterior chamber flat rounded, enclosed in a thick fibrous capsule; posterior chamber small, length shorter than anterior chamber length, less than half eye diameter, thin. Intestine long, complicated, usually coiling.

Distribution. This genus exhibits a relatively extensive distribution. The northernmost boundary is the Heilongjiang River (Amur River) between northeastern China and Far East Russia. The southernmost boundary is the coastal rivers in Fujian Province and northern coastal rivers in Taiwan Province, China. The westernmost boundary is upper reaches of the Yangtze River in Sichuan Province, China, while the easternmost distribution is the west and south coastal rivers of the Korean Peninsula (Fig. 5C).

Etymology. "Micro-" comes from the Greek word "mikrós", meaning small; "physo-" comes from the Greek word "phýsa", meaning bladder. The generic name refers to the reduced swim bladder of the species in this genus. The generic name in Chinese is "小鰾鮈"属, and the Chinese Pinyin name is "Xiǎo Biào Jū" Shǔ.

Species included.

Microphysogobio brevirostris (Günther, 1868).
Microphysogobio chinssuensis (Nichols, 1926).
Microphysogobio yaluensis (Mori, 1928).
Microphysogobio hsinglungshanensis Mori, 1934 (type species).
Microphysogobio koreensis Mori, 1935.
Microphysogobio longidorsalis Mori, 1935.
Microphysogobio amurensis (Taranetz, 1937).
Microphysogobio alticorpus Bănărescu & Nalbant, 1968.
Microphysogobio anudarini Holcík & Pivnicka, 1969.
Microphysogobio springeri (Bănărescu & Nalbant, 1973), comb. nov.
Microphysogobio nudiventris (Lo, Yao & Chen, 1977).
Microphysogobio linghensis Xie, 1986.
Microphysogobio liaohensis (Qin, 1987).
Microphysogobio rapidus Chae & Yang, 1999.
Microphysogobio jeoni Kim & Yang, 1999.
Microphysogobio wulonghensis Xing, Zhao, Tang & Zhang, 2011.
Microphysogobio "*nudiventris*" Jiang, Gao & Zhang, 2012.
Microphysogobio xianyouensis Huang, Chen & Shao, 2016.
Microphysogobio oujiangensis Sun & Zhao, 2022.

Remarks. This study classifies *Platysmacheilus nudiventris* as a *Microphysogobio* species. However, another *Microphysogobio* species described by Jiang et al. (2012) also used the same specific name. Since *P. nudiventris* preoccupied this species name in 1977, the species described by Jiang et al. (2012) requires renaming in the future taxonomic study.

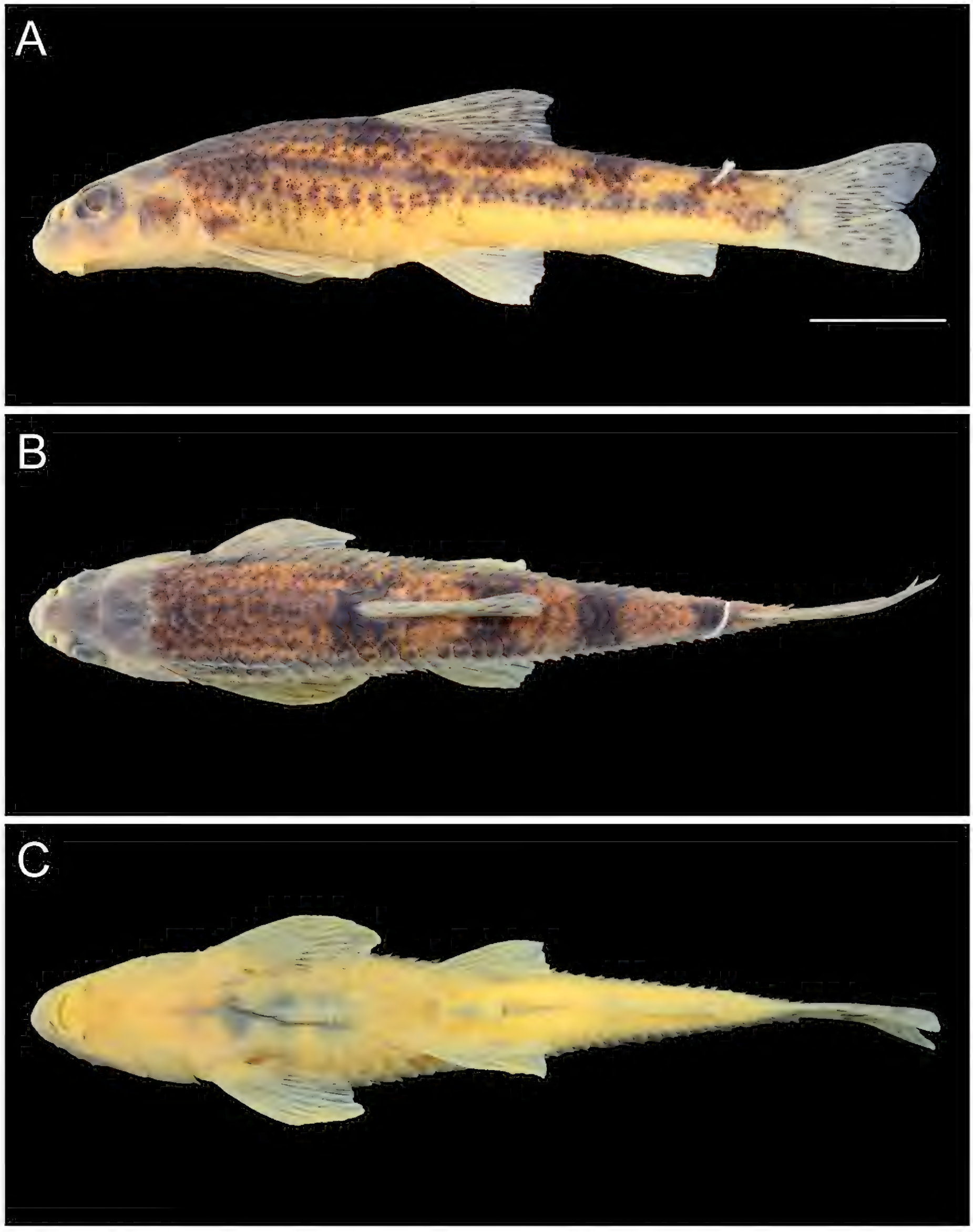

Figure 7. The general view of *Microphysogobio hsinglungshanensis*, the type species of the genus *Microphysogobio*, ASIZB 240788, 51.7 mm SL, collected from the Liuhe River in the Luanhe River Basin, Xinglong County, Hebei Province, China. **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view. Scale bar: 10 mm. Photographed by Zhi-Xian Sun.

Huigobio Fang, 1938

Fig. 8

Huigobio Fang, 1938: 239. Type species: *Huigobio chenhsienensis* Fang, 1938.

Diagnosis. This genus can be distinguished from the other genera within the Pseudogobionini by the combination of the characters: (1) mouth horseshoe-shaped and inferior, forming a sucking-disc structure; (2) central portion of the anterior papillae usually larger than lateral portion of ante-

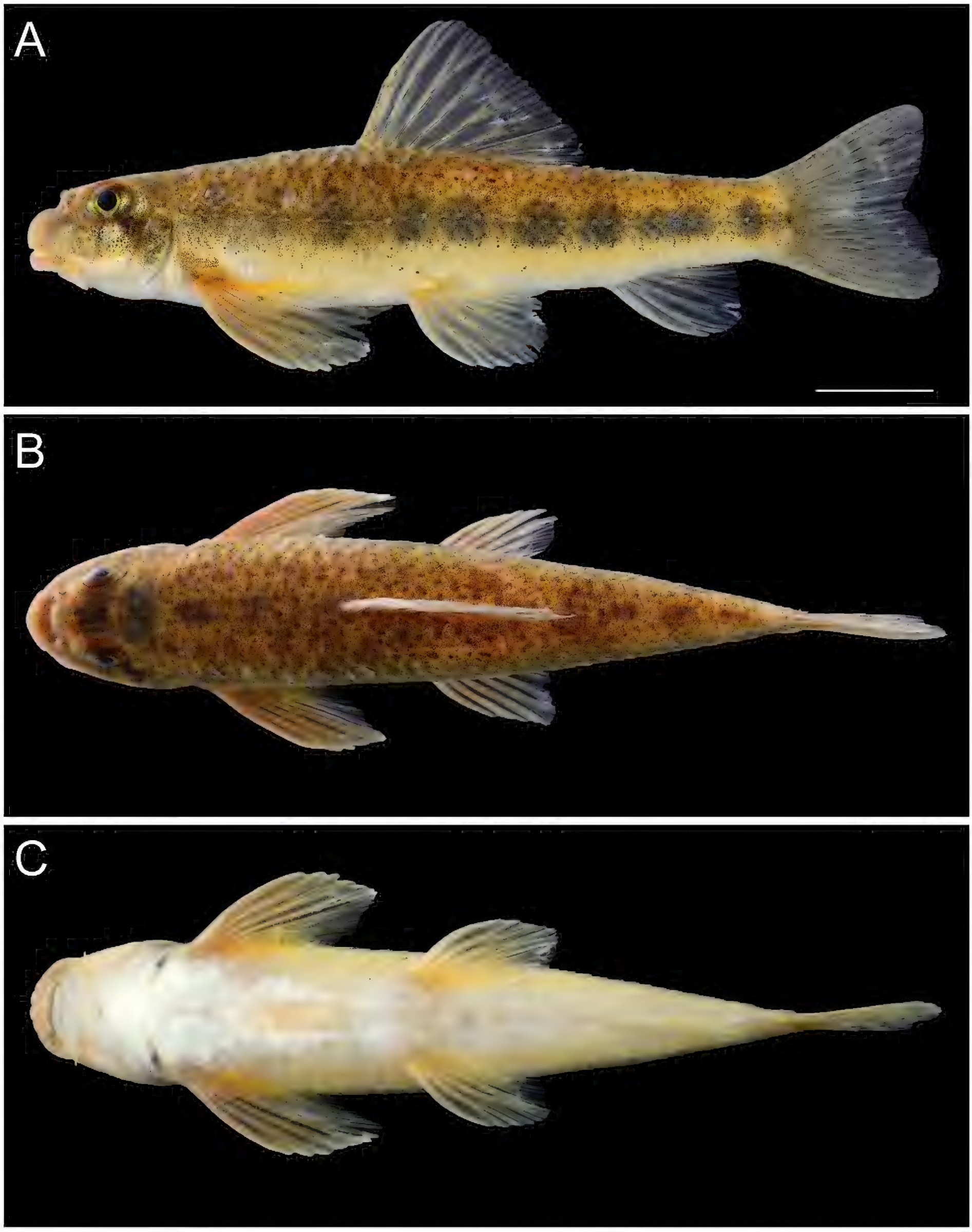

Figure 8. The general view of *Huigobio chenhsienensis*, the type species of the genus *Huigobio*, SHOU 20231209015, 60.4 mm SL, collected from a tributary of the Chengtanjiang River in the Cao'ejiang River system, Shengzhou City, Zhejiang Province, China. **A.** lateral view; **B.** dorsal view; **C.** ventral view. Scale bar: 10 mm. Photographed by Zhi-Xian Sun.

rior papillae on upper lip, more than one row; (3) lower lip usually forming two lateral lobes and a medial pad, without anterior fold; (4) lateral lobes on lower lip contact with each other posteriorly from medial pad; (5) medial pad on lower lip small, heart-shaped, sometimes segmented and fused with lateral lobes; (6) upper jaw wide, the horny margin width larger than half mouth width; (7) lower jaw exposed; (8) barbel in one pair, short; (9) midventral re-

gion of body scaleless or sometimes covered with scales; (10) pharyngeal teeth in one row; (11) anterior chamber of the air bladder enclosed in thick fibrous capsule; (12) posterior chamber relatively small, length smaller than half eye diameter, smaller than anterior chamber length, thin.

Description. Body elongated, abdomen rounded; caudal peduncle short, compressed laterally. Mouth horseshoe-shaped and inferior; barbel one pair; lips thick, with developed papillae; central portion of the anterior papillae usually larger than lateral portion of anterior papillae on upper lip, at least two rows, papillae on second row small, hidden under papillae on first row, lateral portion of anterior papillae in several rows; lower lip usually forming two lateral lobes and one medial pad, without anterior fold; two lateral lobes on lower lip contact with each other posteriorly from medial pad and laterally connected with upper lip anterior papillae around mouth corners; medial pad on lower lip small, heart-shaped, sometimes segmented and fused with lateral lobes. Upper and lower jaws with horny sheathed edge; upper jaw wide, horny margin width larger than half mouth width; lower jaw exposed (Fig. 3C). Body covered with moderately large cycloid scales. Thoracic region scaleless, mid-ventral region covered with scales or scaleless. Anus positioned in anterior one-third of pelvic-fin insertion and anal-fin base. Lateral line complete, almost straight. Lateral-line scales usually 37–40; scales above lateral line 3.5–4.5; scales below lateral line usually 2–2.5; predorsal scales 9–11; circumpeduncular scales 12. Distal margin of expanded dorsal fin slow sloped, straight, with three unbranched and seven branched rays, pectoral fin with one unbranched and 10–12 branched rays, pelvic fin usually with one unbranched and six or seven branched rays, anal fin with three unbranched and five branched rays; caudal fin emarginated, with one simple ray and nine branched rays on upper lobe and eight branched rays and one simple ray on lower lobe, lobes pointed. Pharyngeal teeth "5–5" in one row. Air bladder small, possessing two chambers; anterior chamber flat rounded, enclosed in a thick fibrous capsule; posterior chamber small, length shorter than anterior chamber length, less than half eye diameter, thin. Intestine very long, coiling.

Distribution. This genus exhibits a distribution confined to southern China, including the middle and lower Yangtze River Basin, northern tributaries of the Pearl River Basin, the Qiantangjiang River, Cao'ejiang River, Lingjiang River, and Oujiang River basins. This genus is endemic to China (Fig. 5D).

Etymology. The generic name honors Dr. Hsen-Hsu Hu (胡先骕), the director of the Fan Memorial Institute of Biology, in recognition of his leadership in the development of biological science in China (Fang, 1938). The generic name in Chinese is "胡鮈"属, and the Chinese Pinyin name is "Hú Jū" Shǔ.

Species included.

Huigobio chenhsienensis Fang, 1938 (type species).
Huigobio exilicauda Jiang & Zhang, 2013.
Huigobio heterocheilus Sun, Li, Tang & Zhao, 2022.

Mesophysogobio gen. nov.

https://zoobank.org/48FED4CC-F73B-4490-B7F8-821D6F1ADAA1
Fig. 9

Type species. *Pseudogobio kachekensis* Oshima, 1926.

Diagnosis. The new genus can be distinguished from all other genera within the Pseudogobionini by the combination of the following characters: (1) mouth horseshoe-shaped and inferior; (2) central portion of the anterior papillae small and usually equal-sized, in tight contact with each other, in one row; (3) lower lip forming two lateral lobes and a medial pad, without anterior fold; (4) lateral lobes on lower lip not in contact with each other posteriorly from medial pad; (5) medial pad bisected, heart-shaped, with small papillae or shallow groove; (6) upper jaw narrow, the horny margin width less than half mouth width; (7) lower jaw not exposed, covered by medial pad; (8) barbel in one pair; (9) midventral region of body scaleless only before pectoral-fin base end; (10) pharyngeal teeth in one row; (11) anterior chamber of the air bladder enclosed in fibrous capsule; (12) posterior chamber relatively small, length larger than half or one eye diameter, equal to or slightly larger than anterior chamber length, oval-shaped.

Description. Body elongated, abdomen rounded; caudal peduncle short, compressed laterally. Mouth horseshoe-shaped and inferior; barbel one pair; lips thick, with developed papillae; central portion of the anterior papillae small and usually equal-sized, in tight contact with each other, in one row, lateral portion of anterior papillae in several rows; lower lip forming two lateral lobes and one medial pad, without anterior fold; two lateral lobes on lower lip not in contact with each other posteriorly from medial pad, laterally connected with upper lip anterior papillae around mouth corners; medial pad bisected, heart-shaped, with small papillae or shallow groove. Jaws with horny sheathed edge; upper jaw narrow, horny margin width less than half mouth width; lower jaw not exposed, covered by medial pad (Fig. 3E). Body covered with moderately large cycloid scales. Thoracic region scaleless, mid-ventral region covered with scales. Anus positioned in anterior one-third of pelvic-fin insertion and anal-fin base. Lateral line complete, almost straight. Lateral-line scales usually 36–40; scales above lateral line 3.5–4.5; scales below lateral line usually 1.5–2; predorsal scales 8–11; circumpeduncular scales 12. Distal margin of expanded dorsal fin steep sloped, usually slightly concave, with three unbranched and seven branched rays, pectoral fin with one unbranched and 11–13 branched rays, pelvic fin usually with one unbranched and six or seven branched rays, anal fin with three unbranched and five or six branched rays; caudal fin forked, with one simple ray and nine branched rays on upper lobe and eight branched rays and one simple ray on lower lobe, lobes pointed. Pharyngeal teeth "5–5" in one row. Air bladder relatively small, possessing two chambers; anterior chamber rounded, enclosed in a thick fibrous capsule; posterior chamber relatively small, length larger than half or one eye diameter, equal to or slightly larger than anterior chamber length, oval-shaped. Intestine relatively long.

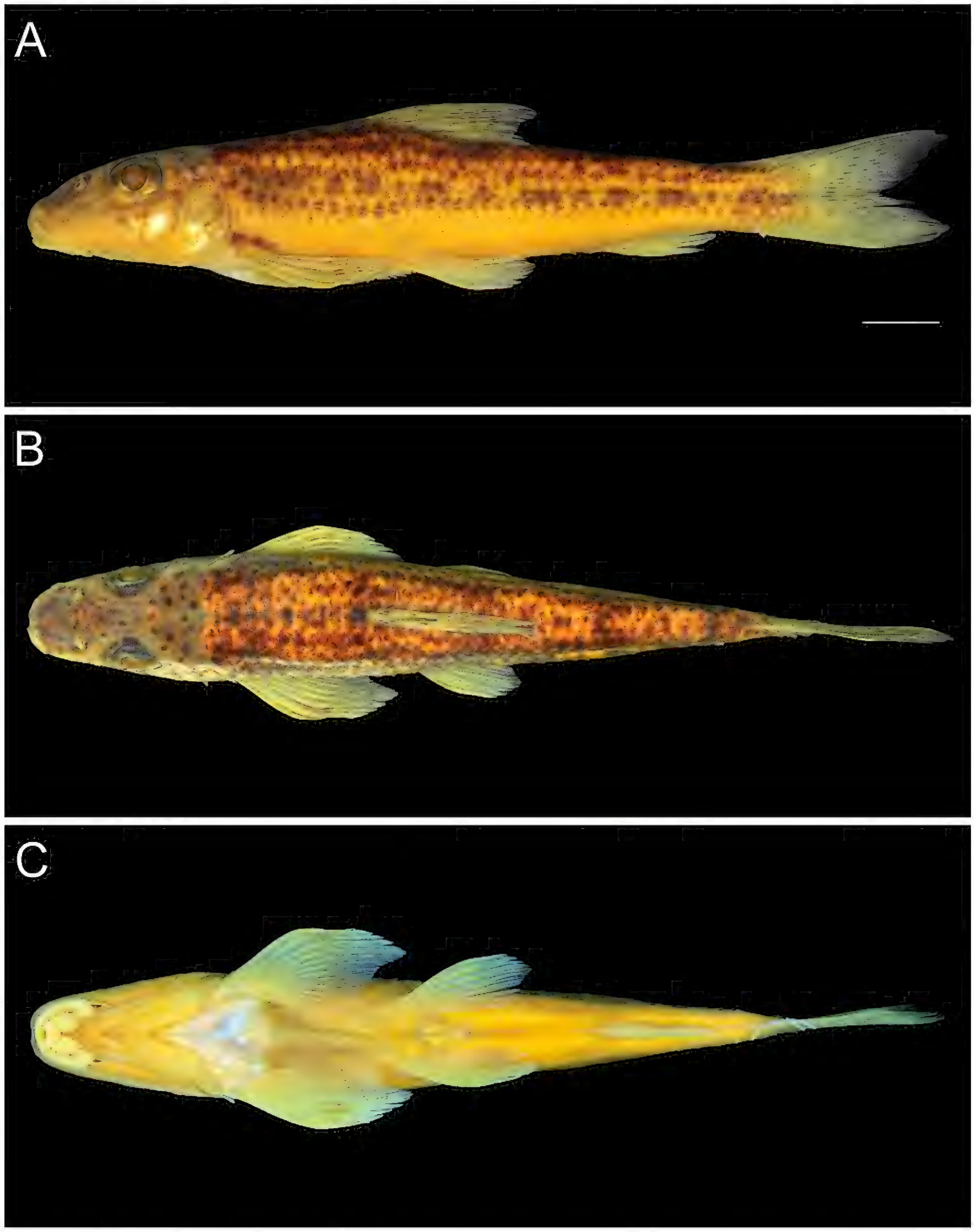

Figure 9. The general view of *Mesophysogobio kachekensis*, the type species of the genus *Mesophysogobio* gen. nov., ASIZB 69768, male, 93.2 mm SL, collected from a tributary of the Dasijiang River in the Maolingjiang River system, Shangsi County, Guangxi Zhuang Autonomous Region, China. **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view. Scale bar: 10 mm. Photographed by Zhi-Xian Sun.

Distribution. This genus is distributed in southern China, including the southern tributaries of the middle and lower Yangtze River, the Qiantangjiang River, the Pearl River, and the Yuanjiang River (Red River) basins, and also the coastal rivers along the southern coastline of mainland China and Hainan Island from the Rongjiang River to the Beilunhe River. It also occurs in the Red River Basin and upper reaches of the Xijiang River (the

longest tributary of the Pearl River) in northern Vietnam and the upper reaches of the Ma River in Laos (Nam Mat and Nam Ma basins, Kottelat, 2001) (Fig. 5H).

Etymology. The prefix "meso-" was derived from the Greek word "mesos", meaning middle, being intermediate; "physo-", from the Greek word "physa", referring to the air bladder. The generic name refers to the medium-sized posterior chamber of the air bladder, which is shared by species within this genus when compared with the genus *Microphysogobio*. The suggested Chinese name for this genus is "中鰾鮈"属, and the Chinese Pinyin name is "Zhōng Biào Jū" Shǔ.

Species included.

Mesophysogobio kachekensis (Oshima, 1926), comb. nov. (type species).

Mesophysogobio bicolor (Nichols, 1930), comb. nov.

Mesophysogobio yunnanensis (Yao & Yang, 1977), comb. nov.

Mesophysogobio luhensis (Huang, Chen, Zhao & Shao, 2018), comb. nov.

Mesophysogobio punctatus (Sun, Tang & Zhao, 2024), comb. nov.

Remarks. Within the *Biwia–Microphysogobio* complex, the new genus *Mesophysogobio* can be distinguished from the genus *Biwia* by having barbels (vs. no barbels) and well-developed lip papillae (vs. thin and simple). It can be distinguished from the genera *Microphysogobio* and *Huigobio* by having a narrow upper jaw horny margin, less than half of the mouth width (vs. wide, larger than half of the mouth width), and a larger posterior chamber of the air bladder, with length usually equal to or slightly longer than the anterior chamber length (vs. tiny, shorter than the anterior chamber length). It can be distinguished from the genus *Platysmacheilus* by having a well-trilobed lower lip (vs. not lobed). It is also different from the new genus *Crossocheilogobio* by having a heart-shaped medial pad on the lower lip (vs. an elongated and narrow medial pad). It is morphologically most similar to the new genus *Oriengobio* in sharing a narrow horny margin on the upper jaw and a one-row central portion of the anterior papillae. However, it can still be distinguished from *Oriengobio* by having a larger posterior chamber, longer than the anterior chamber length (vs. tiny, shorter than the anterior chamber length), an equal-sized and tightly contacting central portion of the anterior papillae (vs. an enlarged and sometimes loosely arranged), and papillae or a groove-covered medial pad on the lower lip (vs. a smooth medial pad).

Platysmacheilus Lo, Yao & Chen, 1977

Fig. 10

Platysmacheilus Lo, Yao & Chen, 1977: 533. Type species: *Saurogobio exiguus* Lin, 1932.

Diagnosis. This genus can be distinguished from the other genera within the Pseudogobionini by the combination of the characters: (1) mouth horseshoe-shaped and inferior; (2) central portion of the anterior papillae small and usually equal-sized, in tight contact with each other, several rows; (3) lower lip without anterior fold; (4) lobes on lower lip formed together, with a notch anteriorly, and free posteriorly; (5) upper jaw narrow, the horny margin width less than half mouth width; (6) barbel in one pair; (7) pharyngeal teeth in one row; (8) anterior chamber of the air bladder enclosed in fibrous capsule; (9) posterior chamber relatively small, length smaller than half eye diameter, thin.

Description. Body elongated, abdomen rounded; caudal peduncle short, compressed laterally. Mouth horseshoe-shaped and inferior; barbel one pair; lips thick, with developed papillae; central portion of the anterior papillae small and usually equal-sized, in tight contact with each other, several rows; lateral portion of anterior papillae in several rows; lower lip without anterior fold; lobes on lower lip formed together, with a notch anteriorly, and free posteriorly. Jaws with horny sheathed edge; upper jaw narrow, horny margin width less than half mouth width (Fig. 3F). Body covered with moderately large cycloid scales. Thoracic region scaleless, mid-ventral region covered with scales. Anus positioned in the anterior one-third of pelvic-fin insertion and anal-fin base. Lateral line complete, almost straight. Lateral-line scales usually 37–39; scales above lateral line 4.5; scales below lateral line usually 2.5; predorsal scales 8–11; circumpeduncular scales 12. Distal margin of expanded dorsal fin steep sloped, usually slightly concave, with three unbranched and seven branched rays, pectoral fin with one unbranched and 11–14 branched rays, pelvic fin usually with one unbranched and seven branched rays, anal fin with three unbranched and six branched rays; caudal fin forked, with one simple ray and nine branched rays on upper lobe and eight branched rays and one simple ray on lower lobe, lobes pointed. Pharyngeal teeth in one row. Air bladder relatively small, possessing two chambers; anterior chamber rounded, enclosed in a thick fibrous capsule; posterior chamber small, length less than half eye diameter, smaller than anterior chamber length, thin. Intestine relatively long.

Distribution. This genus is distributed in southern China, including the middle portions of the Yangtze River Basin and northern tributaries of the Xijiang River (which belongs to the Pearl River Basin). This genus is endemic to China (Fig. 5E).

Etymology. The word "platysma-" derived from the Greek word "platysma", meaning flat object; "-cheilus" derived from the Greek word "cheilos", meaning lip. It means having a flat lower lip. The generic name in Chinese is "片唇鮈"属, and the Chinese Pinyin name is "Piàn Chún Jū" Shǔ.

Species included.

Platysmacheilus exiguus (Lin, 1932) (type species).

Platysmacheilus longibarbatus Lo, Yao & Chen, 1977.

Remarks. This study places two valid species in this genus, the type species *Platysmacheilus exiguus* and *P. longibarbatus*. *Platysmacheilus nudiventris* Lo, Yao &

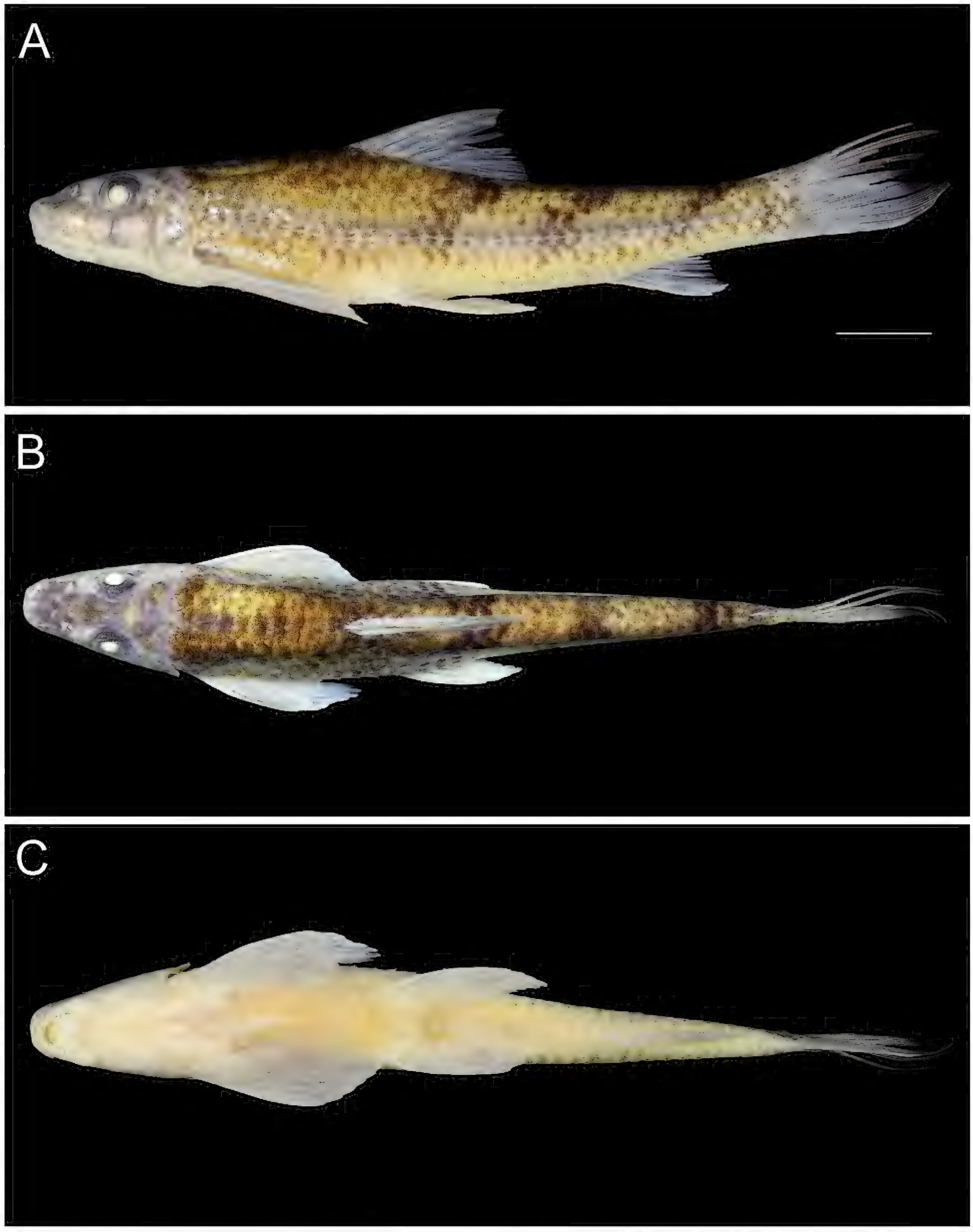

Figure 10. The general view of *Platysmacheilus exiguus*, the type species of the genus *Platysmacheilus*, ASIZB 220879, 77.6 mm SL, collected from the Lijiang River in the Pearl River Basin, Pingle County, Guangxi Zhuang Autonomous Region, China. **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view. Scale bar: 10 mm. Photographed by Zhi-Xian Sun.

Chen, 1977, *P. obtusirostris* (Wu & Wang, 1931), and *P. wangcangensis* Chen, Yang & Guo, 2020 do not belong to this genus because they have significant morphological differences from the type species (e.g., the central portion of the anterior papillae in these three species is in one row; the lower lip is trilobed in *P. nudiventris* and *P. obtusirostris*). This study treats *P. nudiventris* as a *Microphysogobio* species based on its wide upper jaw horny margin and small posterior chamber of the air bladder. *Platysmacheilus obtusirostris* and *P. wangcangensis*,

possessing a narrow horny margin on the upper jaw, a loosely arranged central portion of the anterior papillae, and an exposed lower jaw, should be placed in *Oriengobio* gen. nov. *Platysmacheilus zhenjiangensis* Ni, Chen & Zhou, 2005, collected from the lower Yangtze River in Zhenjiang City, Jiangsu Province, also does not belong to *Platysmacheilus*. It should be a junior synonym of *Oriengobio microstomus* (Yue, 1995), comb. nov.

Oriengobio gen. nov.

https://zoobank.org/D4CFD302-1B28-45E0-A1A8-6DA4A9A01E35

Fig. 11

Type species. *Pseudogobio fukiensis* Nichols, 1926.

Diagnosis. The new genus can be distinguished from all other genera within the Pseudogobionini by the combination of the following characters: (1) mouth horseshoe-shaped and inferior; (2) central portion of the anterior papillae usually larger than the lateral portion of the anterior papillae on upper lip, in one row; (3) lower lip forming two lateral lobes and a medial pad, without anterior fold; (4) lateral lobes on lower lip not in contact with each other posteriorly from medial pad; (5) medial pad bisected, heart-shaped, smooth; (6) upper jaw narrow, the horny margin width less than half mouth width; (7) lower jaw exposed from medial pad; (8) barbel in one pair; (9) midventral region of body usually scaleless before pectoral-fin base end; (10) pharyngeal teeth in one row; (11) anterior chamber of the air bladder enclosed in fibrous capsule; (12) posterior chamber relatively small, length smaller than half eye diameter, thin.

Description. Body elongated, abdomen rounded; caudal peduncle short, compressed laterally. Mouth horseshoe-shaped and inferior; barbel one pair; lips thick, with developed papillae; central portion of the anterior papillae usually larger than lateral portion of anterior papillae on upper lip, in one row, lateral portion of anterior papillae in several rows; lower lip forming two lateral lobes and one medial pad, without anterior fold; two lateral lobes on lower lip not in contact with each other posteriorly from medial pad, laterally connected with upper lip anterior papillae around mouth corners; medial pad on lower lip bisected, heart-shaped, smooth. Jaws with horny sheathed edge; upper jaw narrow, horny margin width less than half mouth width; lower jaw exposed from medial pad (Fig. 3D). Body covered with moderately large cycloid scales. Thoracic region scaleless, mid-ventral region usually covered with scales. Anus positioned in anterior one-third of pelvic-fin insertion and anal-fin base. Lateral line complete, almost straight. Lateral-line scales usually 34–39; scales above lateral line 3.5–4.5 (usually 3.5); scales below lateral line usually 1–2; predorsal scales 8–10; circumpeduncular scales 10–12 (usually 12). Distal margin of expanded dorsal fin steep sloped, usually slightly concave, with three unbranched and seven branched rays, pectoral fin with one unbranched and 9–13 branched rays, pelvic fin usually with one unbranched and six or seven branched rays, anal fin with three unbranched and five or six branched rays; caudal fin forked, with one simple ray and nine branched rays on upper lobe and eight branched rays and one simple ray on lower lobe, lobes pointed. Pharyngeal teeth "5–5" in one row. Air bladder small, possessing two chambers; anterior chamber rounded, enclosed in a thick fibrous capsule; posterior chamber small, length shorter than anterior chamber length, less than half eye diameter, thin. Intestine relatively long.

Distribution. This genus is mainly distributed in southern China and northern Vietnam. The northernmost boundary of the distribution is the Qinling-Dabie Mountains, the southernmost boundary is the upper Xijiang River (the longest tributary of the Pearl River) in northern Vietnam, and the westernmost boundary is the Chengdu Plain in the upper Yangtze River Basin (Fig. 5G).

Etymology. The prefix "orien-" was derived from the Latin for eastern, referring to the Oriental realm in the faunal region. The majority of the species in this genus is distributed in the Oriental realm, which is different from the widespread genus *Microphysogobio*. The suggested Chinese name for this genus is "东洋鮈"属, and the Chinese Pinyin name is "Dōng Yáng Jū" Shǔ.

Species included.

Oriengobio fukiensis (Nichols, 1926), comb. nov. (type species).
Oriengobio tungtingensis (Nichols, 1926), comb. nov.
Oriengobio kiatingensis (Wu, 1930), comb. nov.
Oriengobio obtusirostris (Wu & Wang, 1931), comb. nov.
Oriengobio vietnamica (Mai, 1978), comb. nov.
Oriengobio microstomus (Yue, 1995), comb. nov.
Oriengobio pseudoelongatus (Zhang & Zhao, 2001), comb. nov.
Oriengobio zhangi (Huang, Zhao, Chen & Shao, 2017), comb. nov.
Oriengobio wangcangensis (Chen, Yang & Guo, 2020), comb. nov.

Remarks. The new genus *Oriengobio* can be distinguished from the genus *Biwia* by having barbels (vs. no barbels), a reduced air bladder (vs. enlarged), and well-developed lip papillae (vs. thin and simple). It can be distinguished from the genus *Platysmacheilus* by having a one-row central portion of the anterior papillae (vs. several rows). It can also be distinguished from the genus *Huigobio* by having a one-row central portion of the anterior papillae (vs. two or more rows) and lateral lobes on the lower lip not in contact behind the medial pad (vs. in contact). It can be distinguished from the new genus *Crossocheilogobio* by having a thin rostral cap not semi-covering the central portion of the anterior papillae (vs. thick, semi-covering) and a heart-shaped medial pad (vs. a narrow and elongated medial pad). It is similar to the genus *Microphysogobio* in general morphology. Both genera possess tiny posterior chambers of the air bladder and similar lower lip patterns. However, *Oriengobio* can be distinguished from *Microphysogobio* by having a narrow upper jaw horny margin, less than half of the mouth width (vs. wide, larger than half of the mouth width).

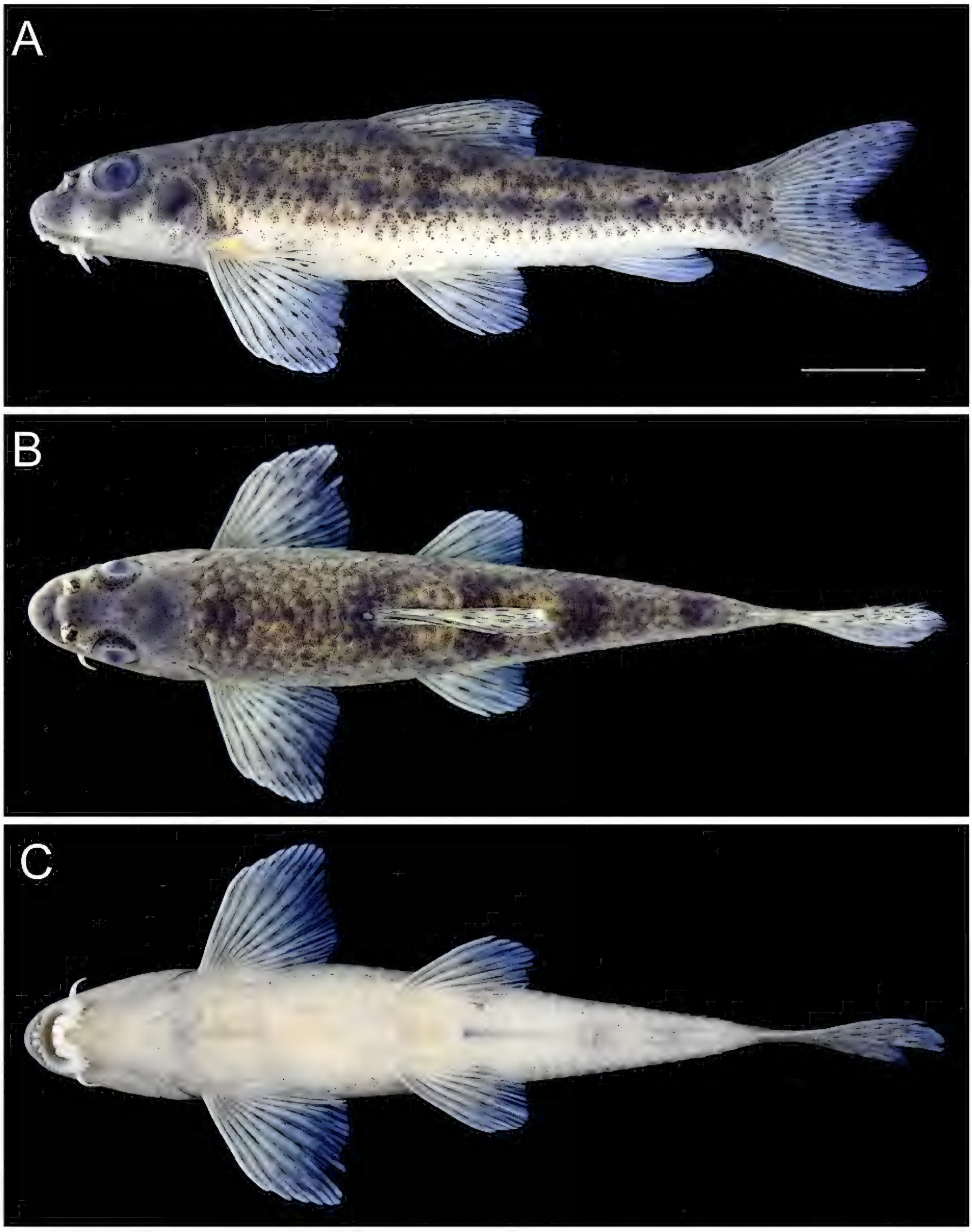

Figure 11. The general view of *Oriengobio fukiensis*, the type species of the genus *Oriengobio* gen. nov., ASIZB 220659, 54.9 mm SL, collected from the Mayangxi River in the Minjiang River Basin, Jianyang District, Fujian Province, China. **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view. Scale bar: 10 mm. Photographed by Zhi-Xian Sun.

Crossocheilogobio gen. nov.

https://zoobank.org/2148D958-5AC8-4F8B-B3F2-0F00ACCC0833

Fig. 12

Type species. *Pseudogobio tafangensis* Wang, 1935.

Diagnosis. The new genus can be distinguished from all other genera within the Pseudogobionini by the combination of the following characters: (1) mouth horseshoe-shaped and inferior, forming a sucking-disc structure; (2) central portion of the anterior papillae two, semi-covered by rostral cap; (3) lateral portion of the anterior papillae on upper lip fringed, in several rows; (4) lower lip in three burred lobes, without anterior fold; (5)

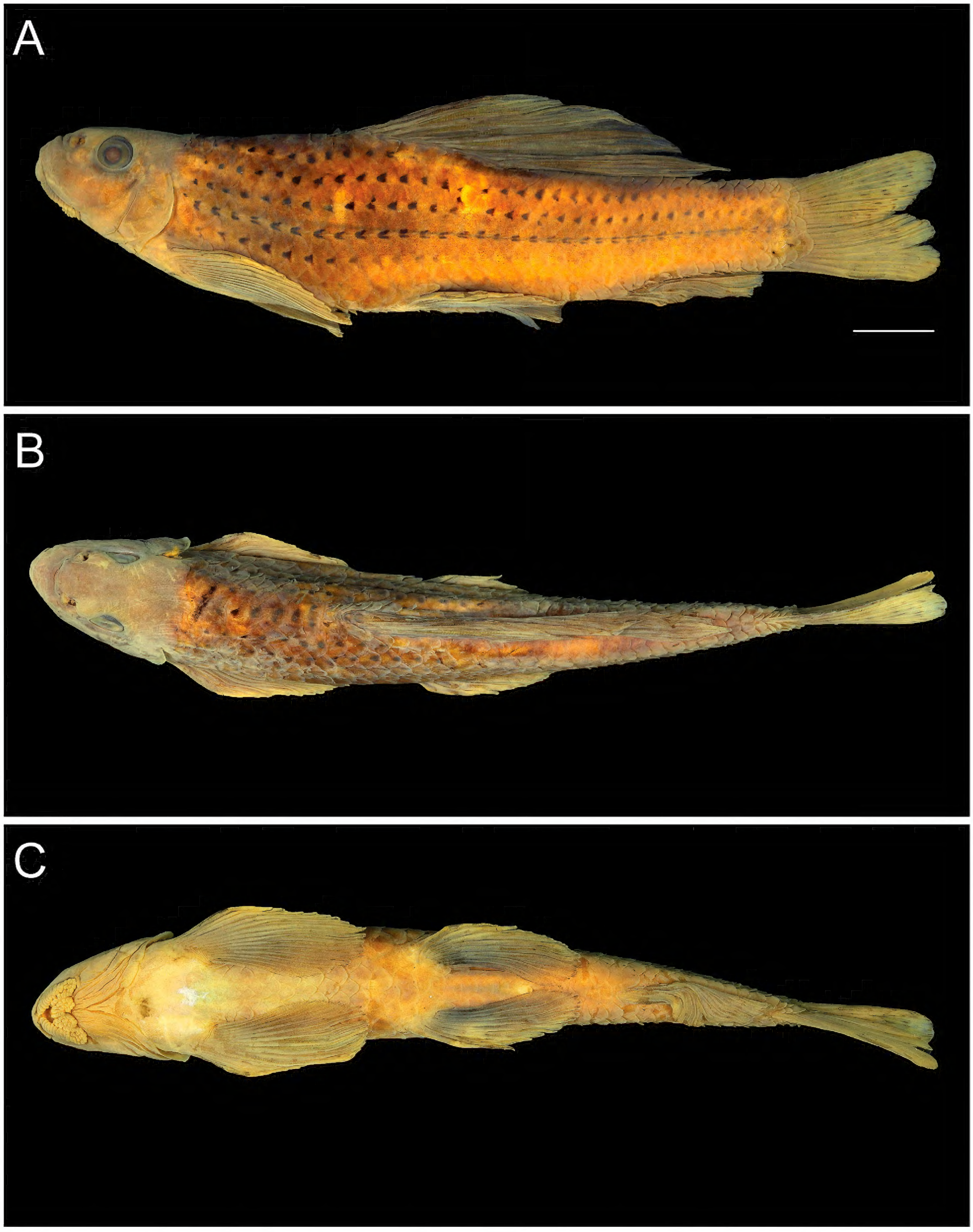

Figure 12. The general view of *Crossocheilogobio tafangensis*, the type species of the genus *Crossocheilogobio* gen. nov., ASIZB 60212, male, 91.2 mm SL, collected from the Xin'anjiang River in the Qiantangjiang River Basin, Tunxi District, Anhui Province, China. **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view. Scale bar: 10 mm. Photographed by Zhi-Xian Sun.

lateral lobes on lower lip not in contact with each other posteriorly from medial pad; (6) medial lobe possessing two elongated thin protrusions; (7) upper jaw extremely narrow, the horny margin width approximately quarter of mouth width; (8) jaws covered by the thick lips; (9) barbel in one pair; (10) midventral region of body usually scaleless before pectoral-fin base end; (11) pharyngeal teeth in one row; (12) anterior chamber of the air bladder

enclosed in fibrous capsule; (13) posterior chamber relatively small, length smaller than half eye diameter, thin.

Description. Body elongated, abdomen rounded; caudal peduncle short, compressed laterally. Mouth horseshoe-shaped and inferior, forming a sucking-disc structure; barbel one pair; lips very thick, with well-developed papillae; central portion of the anterior papillae two, semi-covered by rostral cap, lateral portion of the anterior papillae on upper lip fringed, in several rows; lower lip in three burred lobes, without anterior fold; two lateral lobes on lower lip not in contact with each other posteriorly from medial pad, laterally connected with upper lip anterior papillae around mouth corners; medial lobe possessing two elongated thin protrusions. Jaws with horny sheathed edge; upper jaw extremely narrow, horny margin width approximately quarter of mouth width; jaws covered by the thick lips (Fig. 3G). Body covered with moderately large cycloid scales. Thoracic region scaleless, mid-ventral region covered with scales. Anus positioned in anterior one-third of pelvic-fin insertion and anal-fin base. Lateral line complete, almost straight. Lateral-line scales usually 35–38; scales above lateral line 3.5–4; scales below lateral line usually 2–3; predorsal scales 8–10; circumpeduncular scales 12. Distal margin of expanded dorsal fin convex, especially significant in adult male, with three unbranched and seven branched rays, pectoral fin with one unbranched and 10–13 branched rays, pelvic fin usually with one unbranched and seven branched rays, anal fin with three unbranched and five branched rays; caudal fin forked, with one simple ray and nine branched rays on upper lobe and eight branched rays and one simple ray on lower lobe, lobes blunt. Pharyngeal teeth "5–5" in one row. Air bladder relatively small, possessing two chambers; anterior chamber rounded, enclosed in a thick fibrous capsule; posterior chamber small, length shorter than anterior chamber length, less than half eye diameter, thin. Intestine very long.

Distribution. This genus has a relatively narrow distribution. It is currently known to be distributed in the Qiantangjiang River and Cao'ejiang River basins. This genus is endemic to China (Fig. 5F).

Etymology. The prefix "crosso-" was derived from the Greek word "krossoi", meaning tassel; "cheilo-" from the Greek word "cheilos", meaning lip. The generic name refers to the fringed papillae on the upper lips of the species in this genus. The suggested Chinese name for this genus is "穗唇鮈"属, and the Chinese Pinyin name is "Suì Chún Jū" Shǔ.

Species included.

Crossocheilogobio tafangensis (Wang, 1935), comb. nov. (type species).

Remarks. The new genus *Crossocheilogobio* can be distinguished from the genus *Biwia* by having barbels (vs. no barbels), reduced air bladder (vs. enlarged) and well-developed lip papillae (vs. thin and simple). It can be distinguished from the genera *Microphysogobio* and *Huigobio* by having an extremely narrow upper jaw horny margin, usually quarter mouth width (vs. wide, larger than half mouth width). This new genus is more similar to *Platysmacheilus* in general because their lobes on lower lips are not well separated or even fused. However, the genus *Crossocheilogobio* can be distinguished from *Platysmacheilus* by having central portion of anterior papillae on upper lip in one row (vs. several rows) and a double-lobed medial pad (vs. no obvious medial pad).

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Supplementary material 1

Comparative materials

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Data type: docx
Explanation note: A total of 479 specimens from 28 species in all seven genera within the *Biwia-Microphysogobio* complex are included in this study.
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